Volume 44 Number 3

ANNALS

OF

The Entomological Society of America

SEPTEMBER, 1951

HERBERT OSBORN, *Editor Emeritus*
CLARENCE H. KENNEDY, *Editor Emeritus*

EDITORIAL BOARD

MAURICE T. JAMES, Managing Editor,
PULLMAN, WASHINGTON

1951	1952	1953
A. GLENN RICHARDS, ST. PAUL, MINN.	A. B. KLOTS, NEW YORK, N. Y.	G. S. WALLEY, OTTAWA, ONTARIO.
STANLEY FREEBORN, BERKELEY, CALIF.	P. G. RITCHER, RALEIGH, N. C.	A. B. GURNEY, WASHINGTON, D. C.
WILLIAM C. COOK, WALLA WALLA, WASH.	J. N. KNULL, COLUMBUS, OHIO.	F. M. CARPENTER, CAMBRIDGE, MASS.

PUBLISHED QUARTERLY BY THE SOCIETY
COLUMBUS, OHIO

Entered as second-class matter April 11, 1908, at the Post Office at Columbus, Ohio, under the Act of Congress of March 3, 1879. Subject to rate of postage provided for in Paragraph 4, Section 538, P. L. & R., authorized September 16, 1940.

The Entomological Society of America

Founded 1906

OFFICERS, 1951

President

J. Chester Bradley . . . . . Ithaca, N. Y.

First Vice-President

G. F. Ferris . . . . . Stanford, California

Second Vice-President

H. A. Scullen . . . . . Corvallis, Oregon

Secretary-Treasurer

H. H. Ross . . . . . Urbana, Illinois

Managing Editor Annals

Maurice T. James . . . . . Pullman, Washington

Executive Committee

1951	1952	1953
E. G. Linsley	Melville H. Hatch	S. W. Frost
O. E. Tauber	W. H. Anderson	

Thomas Say Foundation

1951	1952
Willis Gertsch	R. S. Usinger
Alan Stone	C. D. Michener

ANNALS
OF
The Entomological Society of America

Volume 44 SEPTEMBER, 1951 No. 3

OBSERVATIONS ON THE CHIGGER MITE TROMBICULA (EUTROMBICULA) SPLENDENS EWING

(Acarina: Trombiculidae)

KERWIN E. HYLAND, JR.[1]
Department of Zoology, Duke University,
Durham, North Carolina

During a study of rearing technics and feeding habits of trombiculid mites certain observations were made on *Trombicula* (*Eutrombicula*) *splendens* Ewing, 1913 (= *T. masoni*). These observations along with a modified rearing chamber and a new laboratory host are reported herein with the hope that they may be of assistance to other workers in the field.

Facilities incident to the investigation were provided by the Department of Tropical Medicine and Public Health, Tulane University. For advice throughout the study the author wishes to thank Dr. Albert Miller. Thanks are also extended to Drs. Ernest Carroll Faust and Harold Cummins for counsel, and to Dr. George W. Wharton of Duke University for confirming the specific identity of the mites.

MATERIALS AND METHODS

Specimens for study were obtained as engorged larvae from the blue racer snake, *Coluber constrictor flaviventris* (Say, 1823), collected at Shell Beach, Louisiana, October 3, 1948. The host was caged and suspended over a funnel. As the mites became fully engorged and detached they were directed into a culture jar placed under the funnel.

In general and with only minor modifications the rearing containers were made to the specifications of Jenkins (1947). The container consisted of a pint jar with the bottom removed and replaced with a plaster-of-Paris-charcoal plug, on top of which was placed a layer of sterilized soil. A small container or microculture dish was used for closer and more detailed observation of isolated individuals or groups. It was made from the $1\frac{3}{8}$ x $\frac{3}{4}$ inch low-form stender dish in which a $\frac{1}{4}$ inch layer of plaster-of-Paris-charcoal was placed, and on top of that a thin layer of sterilized soil.

[1]Present address: Christchurch School, Christchurch, Virginia.

Eggs of *Anopheles quadrimaculatus* were routinely provided as food for the nymphs and adults. In the pint rearing jars they were usually placed on one or two small pieces of filter paper to facilitate handling; in the microculture dishes they were put in direct contact with the soil.

The American "chameleon" or anole, *Anolis carolinensis* Voigt, 1832, was used as the vertebrate host for larval engorgement. For infesting the host with mites a small wire cage was devised to house the lizard inside the rearing container instead of applying the unengorged mites directly to the host (Michener, 1946) or placing the host on top of the container (Jenkins, 1947). This cage consisted of a wire screen cylinder (18 x 14 mesh, .011 gauge) four inches long, one inch in diameter and closed at one end. The cylinder was soldered to the underside of the culture jar lid and encompassed a ¾ inch hole which had been made in the center of the lid. Thus, by inserting a cork of appropriate size into the hole it was possible to confine a lizard to the cage. Small strips of bond paper were cemented to the bottom of the cage with an acetate-type cement. These strips were allowed to touch the substrate, thus affording the unfed mites an opportunity to reach the host. The host was allowed to remain in the culture jar a varying length of time depending upon the concentration of unengorged larvae in the container and the rate at which these parasitic larvae entered the cage and attached to the host.

After the mites had attached the cage was removed from the jar and transferred (with the lizard) to a new container. When the larvae engorged and dropped from the host they fell through the wire screen directly onto the soil below. Contamination of the substrate with droppings was rarely observed and did not present a problem.

OBSERVATIONS

Various substances have proved to be satisfactory experimental food for nymphal and adult trombiculids. Most of those reported have been eggs of various species of mosquitoes, but Wharton (1946) and Wharton and Carver (1946) indicated that *Euschöngastia indica* (Hirst, 1915) also fed upon eggs of *Drosophila melanogaster* and *Tribolium castaneum*, and on eggs and first stage larvae of the ant *Anoplolepis longipes*. In addition, Jayewickreme and Niles (1946) reported that adults of *Trombicula acuscutellaris* Walch, fed on isolated gravid mosquito ovaries and on a dead intact gravid mosquito; later (1947) they reported feeding adults of this mite on recently killed collembolans and psocids.

It was felt that some of the findings of Jayewickreme and Niles might be applicable to *T. splendens*. Gravid ovaries of *A. quadrimaculatus* were dissected out and immediately offered to four adults and one nymph. At first the mites seemed to ignore the ovaries, but in approximately ten minutes one adult was seen to insert its chelicerae into the mass and begin the hysterosomal contractions associated with feeding. A few minutes later the nymph began to feed, and within fifteen minutes all mites were feeding.

Ovaries that were developing but not gravid were also offered to adults; no feeding was observed. Gravid mosquitoes with legs and wings removed but otherwise intact were offered, but no feeding took

place, nor was feeding observed when female mosquitoes with only partially developed ovaries were offered to five adult mites.

Wharton (1946) and Wharton and Carver (1946) had already reported failure in the use of nematodes as food for *E. indica*. However, two observations were made with *T. splendens*, one using nematode eggs and the other nematode larvae. Several hundred eggs of the human roundworm, *Ascaris lumbricoides*, were offered three nymphs isolated in microculture dishes. No apparent feeding took place and all the nymphs were dead within twenty-four days. One rearing container had been contaminated previously with the feces of the snake from which the engorged chiggers were collected. From the feces hatched many larval nematodes. When the larval mites transformed to nymphs they were offered only the nematode larvae as a possible food. Feeding on these helminths was not observed and further development failed to occur.

Freshly deposited eggs of the tick *Dermacentor venustus* Marx, 1897 (= *D. andersoni*) were offered to four adults which had been without food for ten days. The eggs were placed on the soil in the microcultures with the mites and were examined daily to determine if the mites had pierced the shells. During an eighteen day period no feeding or attempted feeding on the tick eggs was seen. Observations were discontinued at this time because the eggs had begun to hatch. Eggs of *A. quadrimaculatus* were then offered the mites and immediate feeding took place.

For an estimate of how many mosquito eggs might be consumed per day, three adults which had been starved for seven days were isolated each in a microculture dish and fed eggs of *A. quadrimaculatus*. Eggs were added daily and the number of eggs collapsed was determined for a period of thirteen days. Controls were run simultaneously to rule out normal collapsing. One, a female which continued to lay eggs throughout the observations, ate an average of thirty mosquito eggs per day and oviposited a daily average of 6.3 eggs. The other two, which did not lay eggs, consumed an average of 3.4 and 6.0 mosquito eggs per day respectively.

The larvae of *T. splendens* are generally red in color, but during this investigation laboratory reared larvae were light yellow. Larvae from the blue racer snake taken in the field were red insofar as noted, and gave rise to red-colored nymphs and adults (Coral red and Jasper red respectively according to Ridgway, 1912). All larvae hatching from eggs laid by these adults were not red in color but were instead light yellow (warm buff of Ridgway). In every container, including microcultures, in which larvae were produced, this color change occurred. Larvae permitted to engorge on *Anolis carolinensis* showed no noticeable change in color and the engorged individuals dropped from the host still retaining the light yellow color.

The nymphs and adult mites passed their entire free-living stages on a diet of *A. quadrimaculatus* with the exception of those in one container which received eggs of both *A. quadrimaculatus* and *Aedes aegypti*. All cultures were kept under similar environmental conditions.

At the time this color difference was noted all wild caught larvae had metamorphosed into nymphs or adults so that a direct comparison

of the two generations was impossible. Both generations of adults were similar in color.

DISCUSSION AND CONCLUSION

Anolis carolinensis proved to be a satisfactory laboratory host for engorgement of the larvae of *T. splendens*. This animal was easily handled and because of its size made possible the construction and use of a special infestation-engorgement cage. It seems particularly well adapted for use in small scale rearing technics, but for large scale production of chiggers a more sizeable host would probably prove more satisfactory. The chiggers ordinarily completed their engorgement on this host within four days.

Of the several foods offered to the nymphal and adult mites as possible substitutes for mosquito eggs, only the isolated gravid ovaries of *A. quadrimaculatus* were eaten. Factors which play a role in the selection of food substances by the mites have not been determined.

Larvae of *T. splendens* collected from the naturally infested host were red in color and gave rise to red-colored nymphs and adults, but the offspring were all light yellow in color instead of the expected red. The factors underlying such a color variation in the trombiculid mites have not been satisfactorily explained.

Jenkins (1949a, b) reported collecting "albino" forms in the southern United States during chigger surveys and also the occurrence of light forms in laboratory cultures. He suggests that the character is produced by a genetic albino factor. For the present study, however, this explanation appears unsatisfactory for several reasons. (1) Approximately 50 adult females which were reared from red larvae were responsible for the light colored offspring. (2) One hundred percent of the larvae produced were light in color. (3) In routine survey work the collection of light-colored larvae is considered somewhat rare. (4) It seems improbable that a host would acquire 400 to 500 larvae (as in the snake from which the specimens were taken) within an area over which the offspring of a single female might be distributed. (5) Nymphs and adults developing from the light forms regained the apparently normal red color.

If these reasons are considered collectively it becomes evident that a genetic factor is unlikely to be responsible for the color change although it is not definitely ruled out. Unfortunately the cultures were not cared for properly during a change in the author's location and as a consequence all mites died before a second generation was produced.

Inasmuch as all the larvae were collected from the single host, were reared under similar environmental conditions, and received the same food in the freeliving stages there is a suggestion that the responsible factor may be found here.

Wharton (1946) showed a correlation between food and the color of nymphs and adults of *Euschöngastia indica*, and he believes that the color might be attributed to the type of food provided. Nymphs and adults fed on eggs of either *Drosophila melanogaster* or *Tribolium castaneum* were light in color and resembled those collected in nature while those fed on eggs of various mosquitoes produced dark colored individuals. This is a more direct relationship than with *T. splendens*

in which larvae hatching from the egg showed the color change. However, it is conceivable that the food of the nymphs and adults or of the previous larvae (blue racer snake) may influence the color of subsequent developmental stages.

Mosquito eggs are generally used for maintainance of the free living stages of *T. splendens* in the laboratory. If the food of these stages would influence the color of the larvae then this mass color variation would be common occurrence. But this apparently is not the case. The remaining possibility is that of the larval food (host). This appears not to have been investigated, but seems to warrant further study, particularly in light of the present findings.

LITERATURE CITED

Jayewickreme, S. H., and **Niles, W. J.** 1946. Successful feeding experiment with an adult trombiculid mite (Order Acarina). Nature, 157: 878.

1947. Rearing of *Trombicula acuscutellaris* Walch. Nature, 160: 578.

Jenkins, Dale W. 1947. A laboratory method of rearing chiggers affecting man. Ann. Ent. Soc. Amer., 40: 56–68.

1949a. Trombiculid mites affecting man. III. *Trombicula* (*Eutrombicula*) *splendens* Ewing in North America. Jour. Parasitol., 35: 201–204.

1949b. Trombiculid mites affecting man. IV. Revision of *Eutrombicula* in the American hemisphere. Ann. Ent. Soc. Amer., 42: 289–318.

Michener, C. D. 1946. A method of rearing chigger mites (Acarina, Trombiculinae). Amer. Jour. Trop. Med., 26: 251–256.

Ridgway, R. 1912. Color standards and color nomenclature. Washington, D. C.

Wharton, G. W. 1946. Observations on *Ascoschöngastia indica* (Hirst 1915) (Acarinida: Trombiculidae). Ecol. Monog., 16: 151–184.

Wharton, G. W., and **Carver, R. K.** 1946. Food of nymphs and adults of *Neoschöngastia indica* (Hirst 1915). Science, 104: 76–77.

INSECTS IN YOUR LIFE, by C. H. CURRAN. 316 pages, 16 plates. Sheridan House, New York. 1951. Price, $3.50.

Dr. Curran has proven, by his ventures into the semipopular article and book field, that he can write entertainingly as well as in the technical jargon of the taxonomic dipterist. In the present book he discusses a wide range of entomological subjects, including many in the economic field. His accounts of the clothes moths, carpet beetles, termites, ticks, and other arthropods of economic importance, are by no means the dry reading of the usual texts and reference books. Facts are clearly stated and technicalities avoided. The subject matter does not deal entirely with the economic field, but does, in justification of the title, associate the material considered with the human interests, even though those interests by only of curiosity.

Much of the material presented is common knowledge to the professional entomologist, for example, the life histories and habits of ticks, of the yucca moth, and of the human bot fly; but to the layman (and the book is especially directed to him) these are stories as interesting as fiction. Some original and previously unpublished observations and theory are injected into the book, however; for example, the author's identification of the "blue tail fly" of ballad fame with the horsefly, *Tabanus atratus*. Many other phases of insect life are considered, such as butterfly migrations, maternal and paternal care, the use of insects, intentionally or unintentionally, as food, and the flight mechanism of the drone fly.

The publication of a readable, interesting popular work by an entomologist of established reputation is an important event. Entomology has received too little favorable popularization.—M. T. J.

POPULATIONS AND HIBERNATING CONDITIONS OF THE ANT APHAENOGASTER (ATTOMYRMA) RUDIS EMERY[1]

(Hymenoptera: Formicidae)

MARY TALBOT
Lindenwood College,
St. Charles, Missouri

This paper concerns populations of the ant *Aphaenogaster rudis* Emery studied at St. Charles County, Missouri, during 1947–1949. All collections were made in the autumn, winter, and spring, and thus the paper supplements a summer study of *Aphaenogaster rudis* made by A. E. Headley in northern Ohio (Headley, 1949), giving together a year-around picture of their nesting conditions, maturing of brood, and hibernation.

Seventy-one colonies were collected in a small mixed oak-hickory wood. This seemed to be an excellent habitat, and colonies were so plentiful that most of them were collected in a small area, a pawpaw grove shaded by large red oaks and sloping to a small stream. The wood in general was a mixture of red and white oak, hickory, elm, hackberry, walnut, linden, cherry, crabapple, and pawpaw. There was a thick shrub growth of coral berry and blackberry, while vines of wild grape, green brier, and five-leafed ivy made a tangle in the more open places. In more shaded parts the herb layer consisted mostly of spring flowers such as jack-in-the-pulpit, green dragon, spring beauty, wild hyacinth, Dutchman's breeches, sessile trillium, and toothwort. The ground was covered with thick layers of leaves, mostly oak, forming a matting in which the ants frequently constructed aboveground chambers. Beneath the leaf layer the ground was loose and black and filled with numerous runways and earthworm holes. Farther down it became firmer until at six or eight inches it was solid clay. There were no stones in the soil, but roots were numerous.

Nesting conditions and nest structure. Nests are not very extensive. Often there is a simple circular entrance, about one-fourth of an inch in diameter, leading to a central gallery, which may extend straight down or at an angle and from which will radiate from one to nine chambers. These are little domed cavities about one-half inch high and from one-half inch to one-and-a-half inches long. The nests in Missouri seemed in no way dissimilar to those described and diagrammed by Headley except that they were not as large. There was a mean of three chambers (in contrast to his 6.5) and the range of chambers was from one to nine. Nests were also not so deep, averaging 4.85 inches, in contrast to an average of 9.03 in Ohio. The deepest any ants were found was 19 inches, and many nests had no depth at all since they

[1]Formerly *Aphaenogaster fulva* ssp. *aquia* Buckley. The new name follows Creighton's *The Ants of North America*, April, 1950.

were above the soil in layers of leaves or bits of wood. Time of year seemed to have no influence on the number of chambers, but depth of nest did vary with the season, for in March-April the mean depth was 1.71 inches, in May 3.09, in September 5.50, in October 10.83, and during hibernation 10.83 inches. It was not known whether temperature or moisture was primarily responsible for this moving up in the spring and down in the fall, for during autumn the ground tended to be fairly dry while in spring it was soaking wet. Headley found a similar tendency for nests to be more shallow in early summer and deeper in late summer.

Variations in nesting habitat may be summarized as follows: one-third of the colonies nested in soil only, fifteen had one or two chambers among matted leaves and the rest below ground, seven colonies spread chambers among matted leaves and bits of bark and soil, seven nested in decaying branches or bark only, six colonies were simply between layers of leaves, five colonies had some chambers in soil and some in roots, two lived partly in a log and partly in the leaves under it, and one had chambers exclusively in a root.

Populations. The number of individuals making up a colony varied tremendously, from one young colony of only 34 ants to a huge group of 3445 (Table I). However, most colonies consisted of under a thousand individuals, and the mean for all 72 was 738.06. This was a little larger than Headley's mean of 656.66. Workers averaged 325.21, pupae 5.45, larvae 160.56, and eggs 245.31 (Fig. 1). It must be remembered that all collections were made during the autumn, winter, and spring and this made proportions quite different from those of summer months. This was especially true for the pupae. By the end of October all of these had emerged as workers, and in the spring no

TABLE I

POPULATION DATA, COLONIES OF *Aphaenogaster rudis* EMERY

DATE	QUEEN	WORKER	PUPA			LARVA	EGG	TOTAL
			Worker	Male	Female			
9–17–49	1	295	5	.....	.....	60	161	522
9–17–49	1	79	14	.....	.....	37	45	176
9–17–49	1	34	10	.....	.....	14	49	108
9–18–48	1	457	25	.....	.....	59	170	712
9–22–49	1	542	4	.....	.....	93	178	818
9–23–47	2	115	.....	.....	.....	33	38	188
9–23–47	1	174	25	.....	.....	113	43	356
9–24–48	1	514	4	.....	.....	52	118	689
9–27–47	1	98	17	.....	.....	59	108	283
9–29–48	1	181	10	.....	.....	98	240	530
9–29–48	1	273	15	.....	.....	92	254	635
9–29–48	1	518	8	.....	.....	77	273	877
9–29–49	.....	339	6	.....	.....	104	252	701
9–29–49	1	26	5	.....	.....	2	.....	34
10– 2–48	2	244	16	.....	.....	138	252	652
10– 2–48	3	687	.....	.....	.....	74	134	898
10– 2–48	1	102	9	.....	.....	32	72	216

TABLE I—(Continued)

DATE	QUEEN	WORKER	PUPA			LARVA	EGG	TOTAL
			Worker	Male	Female			
10- 2-48	1	44	5	.....	.....	37	80	167
10- 6-48	1	159	6	.....	.....	47	86	299
10- 6-48	1	552	.....	.....	.....	103	195	851
10- 9-47	2	587	.....	.....	.....	46	279	914
10- 9-48	1	138	5	.....	.....	92	131	367
10-11-47	1	156	.....	.....	.....	52	111	320
10-13-48	2	454	.....	.....	.....	205	695	1356
10-16-47	1	199	.....	.....	.....	4	22	226
10-20-48	1	501	2	.....	.....	161	588	1253
10-21-47	1	182	5	.....	.....	64	95	347
10-27-48	.....	477	.....	.....	.....	549	1336	2362
10-30-47	1	68	.....	.....	.....	65	129	263
11-10-48	1	232	.....	.....	.....	233	112	578
11-20-47	1	25	.....	.....	.....	27	55	108
11-25-48	1	450	.....	.....	.....	88	342	881
12- 4-48	1	393	.....	.....	.....	230	305	929
1- 8-49	1	121	.....	.....	.....	50	64	236
3- 4-49	1	144	.....	.....	.....	137	141	423
3-25-48	1	85	.....	.....	.....	30	66	182
3-29-48	1	182	.....	.....	.....	23	24	230
3-30-49	1	57	.....	.....	.....	39	43	140
3-30-49	1	120	.....	.....	.....	131	145	397
4- 6-49	1	420	.....	.....	.....	279	538	1238
4- 6-49	1	199	.....	.....	.....	196	224	620
4- 8-48	2	1078	.....	.....	.....	197	447	1724
4- 9-49	3	607	.....	.....	.....	346	794	1750
4-15-48	4	2079	.....	.....	.....	483	654	3220
4-16-49	15	625	.....	.....	.....	311	683	1634
4-16-49	1	179	.....	.....	.....	85	108	373
4-20-49	1	367	.....	.....	.....	183	225	776
4-20-49	2	321	.....	.....	.....	30	43	396
4-22-48	1	943	.....	.....	.....	126	276	1346
4-27-49	1	73	.....	.....	.....	34	22	130
4-27-49	1	306	.....	.....	.....	129	200	636
4-27-49	1	197	.....	.....	.....	45	126	369
4-28-48	1	52	.....	.....	.....	59	73	185
4-28-48	1	292	.....	.....	.....	49	188	530
5- 6-48	2	146	.....	.....	.....	160	561	869
5- 6-49	1	541	.....	.....	.....	180	369	1091
5-11-49	2	256	.....	.....	.....	128	112	498
5-11-49	3	1010	.....	.....	.....	529	962	2504
5-13-48	1	442	.....	.....	.....	349	173	965
5-18-49	2	184	.....	.....	.....	316	279	781
5-18-49	1	137	.....	.....	.....	62	75	275
5-20-48	1	91	.....	.....	.....	240	60	392
5-20-48	1	156	1	.....	.....	183	162	503
5-20-48	1	105	1	.....	.....	179	77	363
5-27-48	2	780	.....	21	33	303	304	1455
5-27-48	1	51	2	.....	.....	33	19	106
5-27-49	4	131	14	.....	.....	237	272	658
5-27-49	1	116	.....	4	1	268	210	600
5-27-49	1	359	.....	38	1	535	166	1100
5-29-48	4	632	12	50	.....	1302	1445	3445
5-29-48	1	211	.....	11	2	276	139	646

larvae pupated until after the middle of May (Headley's work showed pupa production highest in July and August). Egg laying continued into October and seemingly was resumed again by May. The high count of eggs for October and May was greater than any which Headley found for the summer months. Evidently none of the eggs laid in October developed into larvae until next spring. It may be that the larger number of workers in late March and April can be accounted for by the moving together of colonies as they emerged from hibernation. No males or females had matured by the first of June, but during the

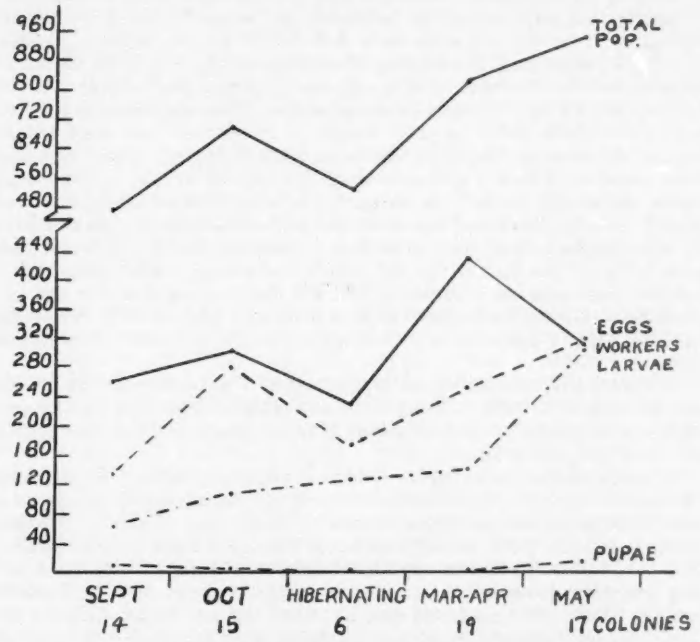


FIG. 1. Means of developmental stages of *Aphaenogaster rudis* Emery during the autumn, winter, and spring.

last week of May male and female pupae were found in five of the seven colonies collected. These were evidently from overwintered larvae and were, in general, developing ahead of the workers. Two of the five colonies also had larger female larvae which had not yet pupated.

Hibernation. Some ants, such as *Prenolepis imparis* Say., do not have a definite hibernating period but may be found foraging whenever the temperature reaches a little above freezing (Talbot, 1943). But *Aphaenogaster rudis* usually stays underground from the beginning of hibernation until its end in the spring. Since it is impossible to find nests during the winter, these were located in the autumn and staked

for winter digging. The first winter (1947–48), this technique resulted in almost complete failure, for, although holes were dug at 12 stakes, only one colony was found. This was probably because nests were staked too early in the fall before it was realized that *Aphaenogasters* do a great deal of moving. Next year staking was begun early in September, and then nests were checked throughout the month and stakes were removed if no ants were seen going in and out of the entrances. By September 20 the ants had abandoned five of twelve staked nests, but this winter five colonies were found and dug.

During hibernation, chambers near the surface were empty, and ants were four inches or more below the surface. In the six nests dug during the two winters ants were distributed at the following levels: nest 1—4 inches; nest 2—4.7 and 10 inches; nest 3—7, 8, 9, 11, 13 and 19 inches; nest 4—11 inches; nest 5—10 and 12 inches; and nest 6—8 and 9 inches; range 4 to 19 inches below ground. The ants were distributed in the chambers about as they would be in summer but were not as easy to see because they did not move until disturbed. In that event some could walk slowly and even tried to carry off larvae. This species overwinters eggs as well as larvae and both of these were scattered among the chambers and lay clustered with the workers. Four of the six colonies had all of their chambers in soil but in one all of the ants were lying on the floor of an old hollow root eleven inches deep and in another there was one chamber in soil at a depth of eight inches and two clusters of ants a foot apart in a hollow root nine inches below the surface. Many collembola and some mites were found with several colonies.

In both 1947 and 1948 the *Aphaenogasters* were hibernating by the second week in October. For several weeks before that they had become harder and harder to find and had traveled more and more slowly as the weather grew colder.

Coming out of hibernation is also a gradual process. In Missouri *Prenolepis imparis* flights seem to mark the beginning of spring since they commence on the first pleasantly warm day (Talbot, 1943 and 1945). In 1948 there had been no warm days until March 19. *Prenolepis* flew on March 19, 20, 24, and 25. (March 21, 22, and 23 were cold and rainy.) *Formica fusca* Linne began coming out of hinernation on March 20, and by March 25, when the wood was visited a few *Aphaenogaster* workers were found walking over the dead leaves. Four days later the ants were still sluggish and moving slowly, and a week after that they were still hard to find. In 1949 *Prenolepis* flew on March 28 and 29 when the first spring beauties and Dutchman's breeches were in bloom. This year the wood was visited on March 30 and *Aphaenogasters* were again found; *Leptothorax curvispinosus* Mayr and *Crematogaster lineolata* (Say) were also emerging from hibernation. But again, for a week or more, workers were hard to find and they moved slowly.

Emergence from hibernation seemed to mean a mass migration for many *Aphaenogaster* colonies. Apparently they reacted to warming temperature by bringing the whole colony, workers, queen, larvae, and eggs, up out of the ground to layers of leaves on the surface or to pieces of wood buried in the leaves. The wetness of the ground in

spring probably was a factor in accelerating this movement. Some colonies retained some chambers underground but many seemed to move entirely away from their hibernating location. There was evidence that colonies tended to mingle at this time, for several huge groups, such as those numbering 3445 and 3220 individuals, were found under slabs of bark. In addition there were often multiple queens, as if several groups might have moved together under a favorable bit of wood. In the fall and winter colonies averaged 1.11 queens and only one had as many as three queens. In contrast, in the spring the queen average per colony was 1.92. At this time 24 colonies had one queen, 6 had 2, 2 had 3, 3 had 4, and one had 15 dealate females gathered together.

A few other species of ants were found during the winter and, since little is known of ant hibernation, it may be of interest to list these.

Ponera coarctata pennsylvanica Buckley—one adult in a little cavity 2 inches deep.

Stigmatomma pallipes Haldeman—one adult and 9 larvae 6 inches down.

Stenamma diecki Emery—one colony of 19 workers and 36 larvae in two chambers ten and fifteen inches deep and a second colony of one queen, 48 workers, and 50 larvae in a chamber ten inches deep.

SUMMARY

Seventy-two colonies of the ant *Aphaenogaster rudis* were dug and counted during the autumn, winter, and spring in a mixed-oak woods in St. Charles County, Missouri. This supplemented a summer survey by A. E. Headley and the two together make a year around study of the ant. Colonies excavated nests in the ground or used layers of leaves or bits of wood aboveground. Nests in the soil had one to nine chambers and averaged 4.85 inches in depth. Populations varied from 34 to 3445 individuals with a mean of 738.06. Eggs and larvae were overwintered, but there were no pupae from the last of October until after the middle of May. During hibernation all ants collected lay between 4 and 19 inches below the surface. Hibernation began by the second week in October and ended during the latter part of March. Colonies seemed to move about considerably and in the spring were apt to gather under logs or slabs of bark in large groups. Males and females developed from overwintered larvae which began to pupate during the last week of May.

LITERATURE CITED

Headley, A. E. 1949. A population study of the ant *Aphaenogaster fulva* ssp. *aquia* Buckley (Hymenoptera: Formicidae). Ann. Ent. Soc. Amer., 42: 265–272.

Talbot, Mary. 1943. Response of the ant *Prenolepis imparis* Say to temperature and humidity changes. Ecology, 24: 345–352.

Talbot, Mary. 1945. A comparison of flights of four species of ants. Amer. Mid. Nat., 34: 504–510.

TEGENARIA AGRESTIS (WALCKENAER), A EUROPEAN AGELENID SPIDER INTRODUCED INTO WASHINGTON STATE

HARRIET EXLINE[1]
Rolla, Missouri

Tegenaria agrestis (Walckenaer) (1802, p. 216) is a widely ranging European species that has been recorded from Germany (Dahl, 1931, p. 43), France and Greece (Simon, 1937, p. 1038), and Russia (Charitonov, 1932, p. 21). It has not been definitely identified in the Americas, although Chamberlin and Ivie (1937), stated that *T. magnacava* Exline (1936, p. 23, fig. 5), described from a unique female collected at Seattle, Washington, "is closely related . . . , if not identical with it." No positive identification could be made without European specimens for comparison.

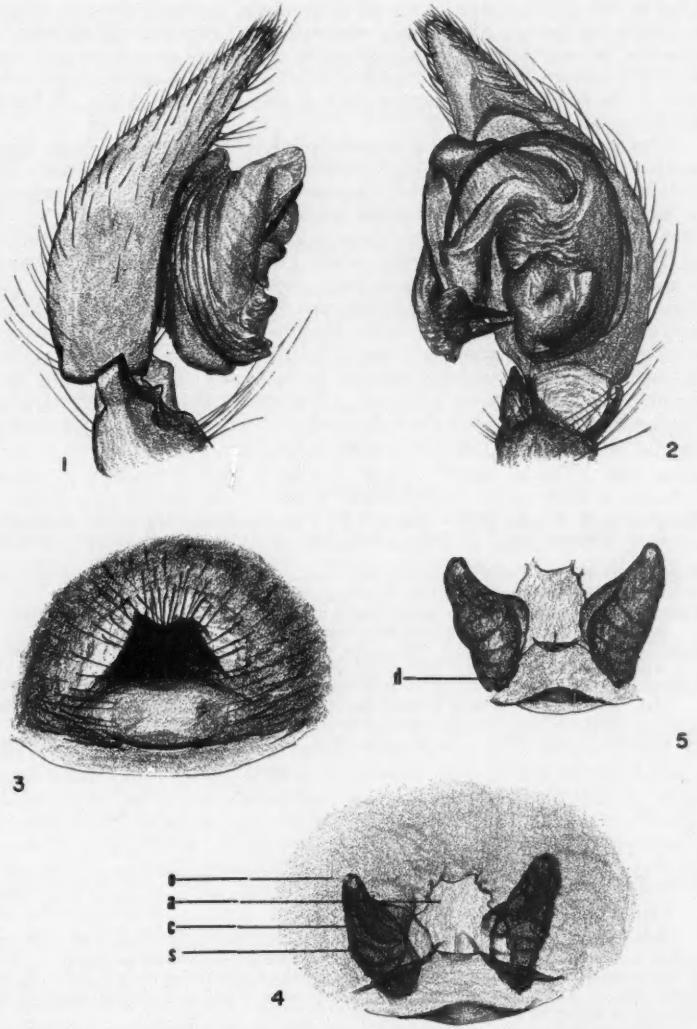
Recently Dr. Hermann Wiehle, Dessau, Germany, has furnished German specimens of *Tegenaria agrestis*. These show that *Tegenaria magnacava* is identical with it, as Chamberlin and Ivie suggested. Several specimens of *T. agrestis* have been collected in Seattle since the holotype of "*T. magnicava*" was found. In August, 1944, a series of males and females was taken in the University District (H. Exline and Mary Ann Nelson). They were living in fairly large webs similar to those of *Hololena*, among cinders built up along the sides of a railroad track. Although the species presumably has been accidentally introduced from European ports through shipping, it appears to have become established at Seattle, probably in recent years.

DIAGNOSIS AND DESCRIPTION OF GENITALIA

Length of females, 10–13 mm.; length of males, 9–11 mm. Body reddish yellow with grayish markings. Chelicerae brown. First three segments of legs yellow, metatarsi and tarsi becoming brownish; legs not annulated. Eyes about equal in size and both rows procurved. Posterior spinnerets long, basal and terminal segments about equal in length. Genitalia diagnostic. Easily distinguished from the cosmopolitan *Tegenaria domestica* (Clerck), and *T. gigantea* Chamberlin and Ivie, but closely related to several European species.

The palpus of the male bears a broad, terminal retrolateral apophysis on the tibia (fig. 1; Dahl, fig. 72 b; Simon, fig. 1537). The conductor is large, with more or less parallel ridges running the length of its external surface and ending ventrally and medially in two long pointed teeth. In the American specimens, these teeth appear to be about equal in length, but the posterior is usually more slender; in the only European specimen examined, the anterior tooth is heavier and longer than the posterior tooth. Both American and European specimens vary some-

[1]Mrs. Don L. Frizzell.



Tegenaria agrestis (Walckenaer), Seattle, Wash. FIG. 1. Right palp, retrolateral view. FIG. 2. Right palp, ventral view. FIG. 3. Female genital plate, ventral view (holotype female of "*T. magnacava*"). FIG. 4. Female genital plate, cleared, ventral view; o, opening between connecting canal and spermatheca; a, atrium; c, connecting canal; s, spermatheca. FIG. 5. Female genital plate, cleared, dorsal view; d, fertilization duct.

what in the position and length of these teeth, and according to Simon (p. 1000) there are occasionally three instead of two. The embolus is heavy, becoming free of the bulb on the prolateral anterior margin and is visible around the anterior part of the bulb; its tip is concealed by a fold of the conductor on the retrolateral side of the bulb (fig. 2; Dahl, fig. 72 a; Simon, fig. 1537).

The genital plate of the female is large, with a very large deep central atrium (fig. 3; Dahl, fig. 71; Simon, fig. 1538). Posteriorly the atrium is limited by a large, thick, horizontal chitinous fold, and laterally by raised chitinous lips. The opening into the connecting tube is not visible in ventral view. Seen from one side, the opening is anterior to the middle of the lateral wall of the atrium. The connecting canal is short, ventral to the spermatheca, swings anterolaterally to enter the anterior part of the spermatheca. The spermathecae are large, heavily chitinous, with thick walls; they lie on each side of the atrium, slanting toward one another posteriorly (figs. 4, 5; Dahl, fig. 71). The interior of the spermatheca appears to be coiled tightly, but the wall possibly may be heavily grooved. The spermatheca is drained from the posterior margin by a short fertilization duct which turns anteriorly and dorsally to empty into the vagina (fig. 5).

REFERENCES

Chamberlin, R. V., and **Wilton Ivie.** 1937. New spiders of the family Agelenidae from Western North America. Ann. Ent. Soc. America, 30 (2), pp. 211–241, 84 figs.

Charitonov, D. E. 1932. Katalog der russischen Spinnen. Acad. des Sci. de l'U.R.S.S., Annuaire du Musée Zoologique, 32, pp. 1–206.

Dahl, Maria. 1931. Die Tierwelt Deutschlands. 23. Spinnentiere oder Arachnoida. 24. Familie: Agelenidae. Jena. Pp. 1–46, 76 figs.

Exline, Harriet. 1936. New and little known species of *Tegenaria* (Araneida, Agelenidae). Psyche, 43 (1), pp. 21–26, 5 figs.

Simon, E. 1937. Les arachnides de France. VI. Synopsis général et catalogue des espèces francaises de l'ordre des Araneae. Pt. 5. Paris. Pp. 979–1298, figs. 1502–2028. (Posthumously published by Berland and Fage.)

Walckenaer, C. A. 1802. Faune parisienne. Insectes. 2. Paris. Pp. 187–250.

THE MICROTOMIST'S VADE-MECUM (BOLLES LEE), Eleventh Edition, by J. Bronte Gatenby and H. W. Beams (Editors). xiv+753 pages. The Blakiston Company, Philadelphia. 1950.

For two-thirds of a century, this remarkable book has been the standard reference for the preparation of biological materials for microscopic study. Prior to the present one, it has gone through ten editions, the latest dated 1937, and one reprinting, in 1946. Some familiarity with it has been a necessary part of the training of every well-rounded biologist.

The present edition, prepared by the editors in collaboration with sixteen contributors, all leaders in their respective fields, has been extensively rewritten. Of course, much of the material has been taken from previous editions, and some extensive parts date back to the original work of Bolles Lee. Some changes reflect the recent advances in techniques, including those developed in Europe during the war years. A new chapter, "Culture Methods for Invertebrata," has been added. Some parts included in the tenth edition have been deleted, and some changes have been made in terminology.—M. T. J.

THE ACTION OF DDT ON THE GOLGI BODIES IN INSECTS NERVOUS TISSUE[1]

PEH-I CHANG[2]
Department of Entomology, University of Illinois,
Urbana, Illinois

INTRODUCTION

The insecticide, 2, 2 bis-(paracholorophenyl)-1, 1, 1 trichloroethane which is commonly known as DDT (dichlorodiphenyltrichloroethane) has proved to be one of the best insecticides ever discovered. Since the war, hundreds of published papers have given us the properties of DDT, such as its chemistry, its toxicity, its manufacture, as well as its application. But there are still many facts about DDT which we do not know. The mode of action of DDT is one of the problems which has attracted many scientists' attention. Up to now, we still do not know exactly how and why DDT kills insects. However we do know that it affects some parts of the insect nervous tissues. Many workers such as Bozkurt (1948), Hartzell (1945), Tobias *et al.*, (1946, 1946a, 1946b) and Welsh and Gordon (1946, 1947) have done histological studies on DDT-treated insects. So far, as the author is aware, no one has studied extensively the internal changes of insect nerve cells that have been treated with DDT. There are, besides others, three important constituents in an insect nerve cell, namely, the Golgi bodies, mitochondria, and Nissl bodies. Anything which causes a change in these three structures could affect the functioning of the whole nervous system. Therefore, the author believes that it is worth while to study the action of DDT on these cell structures to find a way which may help to solve the problem of the mode of action of DDT.

The Golgi body has also been known as Golgi apparatus, Golgi material, lepidosome, lipochondria, dictyosome, and so forth. In the year 1898, Golgi (1898, 1898a) discovered these bodies in the Purkinje cells of the barn owl's brain by means of a method devised by Cajal (Golgi, 1898) for study of nervous tissue. Golgi called them the internal reticular apparatus (appareil reticulaire interne). This apparatus consists of a closed network of fibrils in a rather definite region of the cytoplasm between the nucleus and the cell membrane. In subsequent investigations of a great variety of tissues from many animals, by other scientists, the Golgi bodies usually appear as a group of fibrils lying at one side of the nucleus or entirely surrounding it. The largest and most complex forms are found in vertebrates while the simpler, non-reticulate forms are found in invertebrates, as in insects. They are

[1]Contribution No. 295 from the Department of Entomology, University of Illinois, Urbana, Illinois. This paper is a part of a thesis submitted in partial fulfillment of the Ph.D. degree in Entomology.

[2]The author wishes to acknowledge his thanks to Dr. W. P. Hayes for his excellent supervision and Dr. F. B. Adamstone for his valuable suggestions. Thanks also go to Dr. C. W. Kearns and Dr. V. C. Milum for insect materials from their laboratories.

well developed in active stages of cell differentiation and become less conspicuous as the cell ages. In pathologically or physiologically abnormal tissues, they may show remarkable alterations (Cowdry, 1924).

Cajal (1914) discovered a relationship between the Golgi bodies and the secretion in the goblet cells, in the salivary glands, and in the exocrine pancreas activated by secretion. Cowdry (1922) and Reiss (1922) observed that a reversal in the secretory polarity is accompanied by a movement of the Golgi bodies to the opposite end of the cell. Later, Nassonow (1923) and Bowen (1924), in a series of brilliant investigations, proved conclusively the association of the Golgi bodies with the production of secretion. It was clearly shown by Nassonow, Bowen, and others that droplets of secretion arise in the interstices of the Golgi network, in the intestinal goblet cells, for instance. These droplets grow in number and move gradually toward the distal end of the cell. When the cell is loaded with droplets of secretion, the Golgi bodies break up and the secretion is finally discharged. Since these investigations, many papers have been published suggesting that the Golgi bodies play a significant role in cellular oxidations and reductions, syntheses and hydrolyses, condensations, catalyses, electrical polarization, and other vital phenomena (Kirkman and Severinghaus, 1938). Also, there has been recognized the absorption of vitamin C, iron, copper compounds, gold, and protargal, by the Golgi bodies (De Robertis *et al.*, 1948). Bourne (1942) has given an excellent general review of different aspects of Golgi bodies in his book.

More recently, Emmel (1945) has found that the alkaline phosphatase is concentrated in the Golgi bodies in the cells of intestinal epithelium. Also, Deane and Dempsey (1945) have found the case similar with the acid and alkaline phosphatase in several kinds of epithelial cells. These facts may indicate a participation of the Golgi body in metabolic processes.

All these results show the importance of Golgi bodies. However, De Robertis *et al.*, (1948) have pointed out in their book:

> "Although the existence of a relationship between secretion and Golgi bodies seems to be established, the explanation of this relationship has not yet left the domain of hypothesis. . . . It is safer to affirm that, up to the present time, there is no satisfactory theory to explain in general form and for all cells the function of the Golgi apparatus."

The author used American cockroaches, ***Periplaneta americana*** (Linné) and honeybees, ***Apis mellifera*** Linné for his experiment. The cockroaches are primitive insects, while the bees are highly specialized insects. Both bees and cockroaches are always available throughout the year and their nervous tissue is comparatively easily dissected out for study.

The gamma isomer of benzene hexachloride is known not to be a nerve poison and is highly toxic to insects. The author has used it as a check treatment in comparison with DDT to show the significance of the result.

The present work is only a stepping stone which should lead us to pursue further studies about the effect of DDT on the Nissl bodies, mitochondria, and other cellular elements of different insects tissues. If we can solve all these problems, we may be able to find out how and why DDT kills insects.

REVIEW OF THE LITERATURE

1. *Mode of Action of DDT*

DDT is a slow poison. It may not manifest lethal effects for several hours or days, depending on the methods of treatment and the species of insects. The symptoms of DDT poisoning are nervous action, followed by fine or coarse tremors, flaccid and spastic paralysis, tonic and clonic convulsions, and finally death.

We are still uncertain about the mode of action of DDT. Many investigators have been able to show some histopathological changes in different tissues of different animals, (Carey, 1946; Hartzell, 1945; Nelson, 1944; Roeder, 1946; Welsh, 1946, 1947; Yeager, 1945; etc.). Such changes in mammals as necrosis in the liver, focal necrosis of voluntary muscles, pitting of the kidneys, foci of hemorrhage in the stomach, vacuolation of the nerve cells, disappearance of motor end plates, and granular and various auriphilic substance in the muscles, have been reported. In insects, most people (Richards and Cutkomp, 1945; Bozkurt, 1948) failed to find convincing evidence of histopathological changes. Hartzell (1945) found some signs of the degeneration of nuclei and a slight dissolation of the fiber tracts in the brain and thoracic ganglia of houseflies. Hartzell's work was strongly criticized by Richards and Cutkomp (1945), who stated:

> "Hartzell records relatively slight pathological effects from DDT. He has no real knowledge of whether or not the nerves concerned were living or dead. . . . But the slight effects recorded agree with the usual autolysis picture. We can only repeat that in our DDT experiments dying cockroaches which had responsive nerve cords showed no effects that could not be ascribed to normal variation and matched by control preparations."

According to Richards and Cutkomp's paper, the histopathology of insect nervous tissue may at times give some slight help in localizing the action of certain insecticides, but it is at best a crude and possibly a misleading measure of physiological effects.

Many other workers have worked on the physiological pathology of DDT-treated insects or other animals. Tobias *et al.*, (1946) found no important changes in blood chemistry. However, they (1946a) found that the nerve cord acetylcholine content rises markedly (about 200%) in cockroaches and flies during the latter prostrate phase, but not during the hyperactive phase of DDT poisoning. No evidence was found that DDT poisoning affected the esterase activity. Philips *et al.*, (1946) found that DDT both sensitized the myocardium and caused sympathetic discharges; the latter may be reflex, but more probably are the result of direct hypothalamic stimulation. Ricker *et al.*, (1946) showed that when symptoms of intoxication were present in cockroaches, the increased respiration rate was reflected in the increased oxygen consumption. Welsh and Gordon (1946, 1947) studied the arthropod nerve axon (crayfish, shore crab, lobster, cockroach) and stated that DDT and DDT-analogs and other substances having a high lipid/water solubility ratio, cause a characteristic "multiplication" of nerve impulses. Several lines of evidence indicate that this action is a physical interference at the lipid surface of the nerve axon. Ludwig (1946) worked on the effect of DDT on metabolism of the Japanese beetle; he noticed in the poisoned insects a loss of metabolic

water, an increase in rate of oxygen consumption, and a rapid utilization of carbohydrate reserve. Draize *et al.*, (1945), Richards and Cutkomp (1946), and Campbell (1946) have proved that DDT is taken up by the insects through their cuticle.

Roeder *et al.*, (1946) pointed out that undoubtedly DDT affects motor nerves and muscle fibers of cockroaches, the tremor characteristics of DDT poisoning being due to an intense afferent bombardment of the motor neurones. Roeder thinks that DDT has no significant action on the central nervous system of cockroaches. From a somewhat different experiment, however, Tobias and Kollros (1946) found, in American cockroaches, that the thoracic ganglia are the critical loci for the action of DDT. Bodenstein (1946), in his investigation on the locus of action of DDT in flies (*Drosophila*), stated that only the nervous system of the fruit fly is affected by DDT poisoning. He transplanted larval organs (imaginal discs) which had been exposed to DDT for 24 hours into untreated larvae. These organs grew and differentiated normally. This fact strengthened his conclusion. Bozkurt (1948) concluded in his work that DDT and gamma BHC are taken up through the cuticle, and that they are not dependent on the nerve endings for their absorption. He found no histological change on the head ganglia and nerves of American cockroaches killed by DDT. Hayes and Liu (1947) believed DDT acted on chemoreceptors on the foot of the housefly and there seemed to be thinner cuticula in insects affected by DDT.

From this brief review, we can see how confused is the situation concerning the mode of action of DDT. We still do not know just how and why DDT kills insects. However, we do know that DDT affects the nervous system, as well as the metabolism, and the physiological mechanism of insects.

2. *Mode of Action of BHC*

Benzene hexachloride, or 1, 2, 3, 4, 5, 6-hexachlorocyclohexane is commonly known as *666* or BHC. It has the merit of acting as a stomach poison, as a contact poison, and as a fumigant. It is much more toxic to most insects than DDT. It also works much faster than DDT. The affected insects show convulsions within a few minutes following application and finally become paralyzed and die. The toxic property is due to the gamma isomer of the compound.

According to Slade (1945), the physilogical activity of the gamma isomer of BHC as an insecticide may be due to its antagonism toward the essential metabolite, inositol, which is found in many types of cells. Gamma BHC is very similar to inositol, not only in molecular dimensions, but also in some physical prerequisites. Therefore, it is possible that gamma BHC is absorbed from the outside of the insect, distributed throughout some portion of the organism to the cells where a vital reaction is blocked and the organism dies. Kirkwood and Phillips (1946) confirmed Blade's idea in their work with a yeast Gebrüder Mayer strain of *Saccharomyces cerevisiae*. Their data suggest that the spatial configuration of the gamma isomer is similar to that of i-inositol and further support the hypothesis that the gamma isomer exerts its insecticidal action by interfering with inositol metabolism of insects.

Buston *et al.*, (1948) worked with an ascomycete, *Nematospora gossypii*, which requires exogenous i-inositol, and had observed a similar effect with gamma isomer. McNamara and Krop (1948, 1948a) studied the pharmacology of some stereoisomers of BHC in animals. They observed that the gamma isomer is a potent convulsant agent and the delta isomer is a central nervous system depressant. Moreover, they found that the two isomers are mutually antagonistic in their

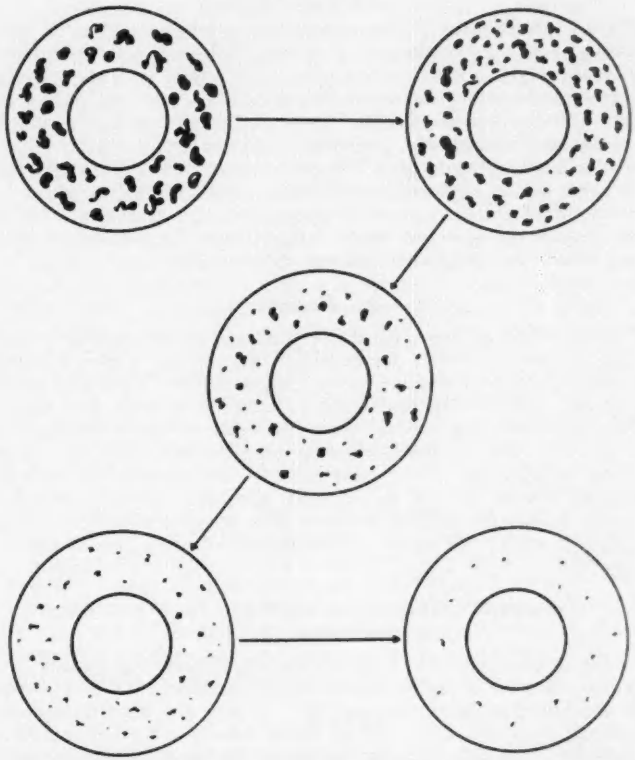


FIG. 1. Diagram of the successive stages of the breakage of the Golgi bodies in insect ganglionic cells.

effects upon the central nervous system of rabbits and dogs. When later (1949) they studied the influence of delta and gamma BHC upon the oxygen uptake of the brain of rats, they found that gamma BHC failed to alter the oxygen uptake of the brain, while the delta isomer significantly increased this function. Inositol did not alter the oxygen

uptake produced by either isomer, and gamma BHC exhibited no antagonism against the effects of the delta isomer.

It seems to be established that the gamma BHC interferes with the metabolism of poisoned insects and other animals. No histological work, so far as the writer is aware, has been done with animals treated with it.

GENERAL STRUCTURE OF THE NORMAL CENTRAL NERVOUS SYSTEM

1. *American Cockroach*

The main structure of the central nervous system consists, chiefly, of a brain, a suboesophageal ganglion, followed by three thoracic ganglia and eight abdominal ganglia. The brain and suboesophageal ganglion are connected with the other ganglia by two longitudinal nerve trunks. The brain and suboesophageal ganglion innervate the antennae, compound and simple eyes, and mouthparts, while the thoracic ganglia innervate the wings and legs. The nerves from each abdominal ganglion go to parts of the segment in which the ganglion had its origin. The last abdominal ganglion innervates the cerci and genital organs. The three thoracic ganglia are much larger than the abdominal ganglia, among which the last abdominal one is the largest.

2. *Honeybee*

The structure of the central nervous system of honeybee is similar to that of the cockroach except that some of the abdominal ganglia are usually fused. There are seven ganglia in the thorax and abdomen (Snodgrass, 1925). The first thoracic ganglion is in the prothorax and is situated above the sternal plate in front of the prosternal furca. The last two thoracic ganglia are combined with the first abdominal ganglion to form the largest ganglion. It lies beneath the arch of the combined furcae of the mesothorax and the metathorax. In the abdomen, there are only five small ganglia, some of which are composite ganglia formed by the union of the ganglia of the adjacent abdominal segments.

GENERAL HISTOLOGICAL FEATURES OF A VENTRAL BODY GANGLION OF INSECTS

A segmental ganglion of the thorax or abdomen is usually an oval or polygonal mass of nerve tissue, continuous anteriorly and posteriorly with the interganglionic connectives. There are some lateral nerves branching from its sides; and in some insects a median nerve arises posteriorly, or also anteriorly between the bases of the connectives. The median nerve is a part of the ventral sympathetic nervous system. The outermost layer of the ganglion is a nucleated sheath, the neurilemma, which is continuous over the connectives and the nerves. Unlike the vertebrates whose principal cellular elements of the ganglion lie in the central portion of the ganglion, in the insects, the principal cellular elements are peripherally located, mostly in the lateral and dorsal parts. The Golgi bodies in these cellular elements of insects were used for study in this paper. The central and ventral parts of the ganglion are occupied by a neuropile mass. In addition, the ganglion

is penetrated by tracheae. Snodgrass (1935) wrote that, according to Zawarzin's (1924) work on the nymph of *Aeschna*, there are five distinguishable regions within the neuropile and six principal groups of nerve elements in each ganglion. It is not necessary for us to go into these details.

METHODS OF PROCEDURE

Generally, the methods of studying Golgi bodies can be classified into three categories, namely, vital or supravital examination, the osmium method, and the silver method. The fact that, generally, the Golgi bodies are not visible *in vivo* has caused many authors to doubt their real existence. This inability to see them is because the Golgi bodies have the same refractive index as the rest of the cytoplasm (De Robertis *et al.*, 1948). However, different investigators have been able to see them in the cells of the prostate, in intestinal cells of *Ascaris*, in Purkinje cells, and in various tissues of the invertebrates (De Robertis *et al.*, 1948). Further, they have been observed in the cells of the seminal vesicle and in the spermatids by means of the phase microscope (Brice, Jones, and Smyth, 1946). With vital or supravital staining by methylene blue, it has been shown that the Golgi bodies can be seen *in vivo*, in many types of cells in both vertebrates and invertebrates (Worley, 1946). This method was not employed in this study. The second method, called the osmium method, is a fixed preparation treated with osmic acid. McClung (1937) introduced five osmium methods devised by Kopsch, Sjavall, Hirschler, Kolotchew, and Gatenby (also see Lee, 1946). Some of these methods require a very precise control of temperature, and some of them require a long period (up to 16 days) of osmic treatment. These two disadvantages influenced the author to abandon the osmium method. The silver method is a method of impregnation, which was originally introduced by Von Recklinghausen in 1860 (Carleton, 1919). The Cajal methods for neurofibrils, and the Golgi and Cajal impregnations for the Golgi bodies, embody the above process (Carleton, 1919). In silver impregnation, the tissues undergo (1) fixation, (2) impregnation, (3) reduction with a modified photographic developer, and (4) toning by gold chloride. The author used Da Fano's (1920) cobalt nitrate silver method which is the most well developed and best adapted method for impregnation. The following are the details of this method.

1. *Material*

The last nymphal instars of the American cockroach and the young adult of the worker honeybee served as the chief materials for this study. The thoracic ganglia of the cockroach and the bee were used as the representative ganglia of the central nervous system of these insects, since the brains of these insects are heavily protected by a chitinous skeleton which can hardly be removed without destroying the brain. In addition to the thoracic ganglia, the last abdominal ganglia of the cockroach were also used. These ganglia, besides the brain, are the only parts of the central nervous system which are large enough to be handled in preparation.

2. *Killing and Fixing*

A. Fixative

Cobalt nitrate	1 g.
Distilled water	100 cc.
Formalin (Full strength, neutral)	15 cc.

This solution can be prepared and kept on hand. It keeps for months without any alteration of its nature (Da Fano, 1920). The author dissolved cobalt nitrate in distilled water in a brown bottle and added fresh formalin to the solution before use. Formalin is usually easily oxidized by the air and forms formic acid which, is some cases, may affect the result, especially when it is strongly acidified. Therefore it is safer to neutralize formalin by shaking it with magnesium carbonate and by filtering it before use. Some formalin may contain free sulphuric acid, in which case, the neutralization is particularly essential.

B. Killing and Fixing for Study in Normal Condition

a. Honeybee. Collect the young worker bees from the hive, then knock them down with carbon dioxide. Cut off the head, abdomen, wings, legs, and the dorsal half of the thorax. Immediately put the ventral half which contains the ganglia into a vial containing the above fixative. There should be about fifteen to twenty halves of bee thoraces in each vial, depending upon the speed of the cutting. Only five minutes between the operation of the first bee and the last bee should be allowed; otherwise, the variation of the time of fixation may cause differences in the results. After the specimens have been immersed in the fixative for about twenty minutes, in order to harden the tissue somewhat, they should be taken out and all the muscles surrounding the ganglion[3] should be removed. Then, in order that the ganglion will have the closest possible contact with the fixative, the dorsal furca which embraces the ganglion should be broken and then removed with a fine needle, using great care to avoid any breakage of the ganglion. After the muscles and the furcae have been removed the specimen should be returned to fresh fixative.

b. American cockroach. Cut off the head and the legs of the nymph. Then remove the dorsal half of the body and the alimentary canal so as to leave only the nervous system and some other tissue attached to the ventral half of the body which is later pinned on a paraffin dissecting dish. As soon as the specimen is pinned on the dissecting dish, place a few drops of fixative on the specimen and begin to cut off the muscles covering the nervous system. Then cut off the nerves branching out from the ganglia and remove the fat tissues and the tracheae in order to free the thoracic and abdominal ganglia which are connected by two longitudinal connective nerves. The last step is to put the whole series of ganglia into a vial of fixative. Put the ganglia of four or five cockroaches in each vial. The work time for each vial of material is limited to 10–15 minutes.

[3]The ganglion here means the second ganglion in the thorax. The first, or the cephalic one, is too small to handle, is easily overlooked and may be removed with the discarded muscle tissue.

C. DDT Treatment

a. Honeybee. Smear 10% technical DDT in acetone on the inside of a cylindrical paper carton with a screen cover on each end and confine the bees in it. The bees will be killed within four to seven hours. Divide the treated bees into three groups, namely, knockdown, morbid, and dead bees. Fix each group of bees as described above.

b. American cockroach. Inject about 50 micrograms of technical DDT (6% acetone solution) into the abdomen of the nymph of each cockroach with a micrometer-operated syringe. When they are knocked down, or become morbid or dead, then dissect out their ganglia for fixation. DDT always acts slowly on cockroaches. Usually cockroaches are knocked down after about five to eight hours, become morbid within two or three days, and die within three to five days, depending upon the physical condition of the individual cockroaches. Each time, we should treat as many cockroaches as possible in order to select cockroaches of the same condition for each group.

D. BHC Treatment

a. Honeybee. Same as DDT treatment, only use 6% technical BHC instead of DDT.

b. American cockroach. Put some dry technical BHC into a glass jar and confine approximately thirty cockroach nymphs into it; then shake the jar for a few seconds. The contact action of BHC will kill the nymphs. The treated nymphs are also fixed into three groups, knockdown, morbid, and dead.

E. Time of Fixing

The time of fixation is very critical. Underfixing or overfixing will not show Golgi bodies in the resulting preparations. The author had much difficulty with this problem; however, he found that the proper time of fixation for bees is two hours and twenty minutes, and for cockroaches is four hours.

3. *Impregnation*

After the material is fixed, then it is washed briefly with distilled water, and is put into an aqueous solution of silver nitrate. The impregnation should be done in total darkness. If the silver nitrate solution becomes dark, it should be replaced by fresh solution immediately. The strength of silver nitrate is 0.75–1% for bees, and 1–1.5% for cockroaches. The duration of impregnation is 24–48 hours for both bees and cockroaches.

4. *Reduction*

When impregnation is completed, the material should be washed with distilled water twice and should be put into Cajal's reducing agent for 12–24 hours. Cajal's agent is composed of:

Hydroquinone (or pyrogallic acid)	1–2 g.
Neutral formalin (full strength)	5–10 cc.
Distilled water	100 cc.

As this solution does not keep well, it should be freshly prepared. Prolongation of the reducing period is not necessary, although it does

not harm the tissue (Da Fano, 1920). The author prefers a period of overnight. After reduction, the material should be washed in several changes of distilled water for half an hour.

5. *Dehydration*

Dehydrate the material in 30%, 50%, 70%, 80% 95%, and 100% ethyl alcohol for one to two hours in each solution. When in 80% alcohol, the ganglia of bees should be removed from the thorax, and the three thoracic ganglia and last abdominal ganglia of the cockroaches should be cut off from the longitudinal connective nerves. Then put the free ganglia into the next alcohol and so on.

6. *Clearing*

Clear the material with cedarwood oil over night. The author found this a better clearing agent than xylol, chloroform, and olive oil. Xylol is a commonly used solution, but it is easily acidified through the oxidization of the air so that it usually destroys the impregnation at a higher temperature.

7. *Infiltration, Imbedding, and Sectioning*

The cleared material is then infiltrated with 56–58° paraffin for at least six hours, imbedded, sectioned (6 microns), and affixed on the slides with albumen.

8. *Staining or Toning*

Run the slides from xylol, absolute alcohol, and graded alcohols down to distilled water, then stain the slides with 0.1% gold chloride for one and one-half hours and counterstain with alum carmine for half an hour or less. After dehydration and clearing, the material is mounted in Canadian balsam for observation. Staining with gold chloride is also called toning, which will give the material a permanent preservation.

RESULTS[4]

1. *Structure of Golgi Bodies in Normal Ganglionic Cells*

In the American cockroach (fig. 2), the Golgi bodies, dispersed in the cytoplasm between the nucleus and the cell wall are numerous, coarse, granular structures with various shapes, such as kidney, egg,

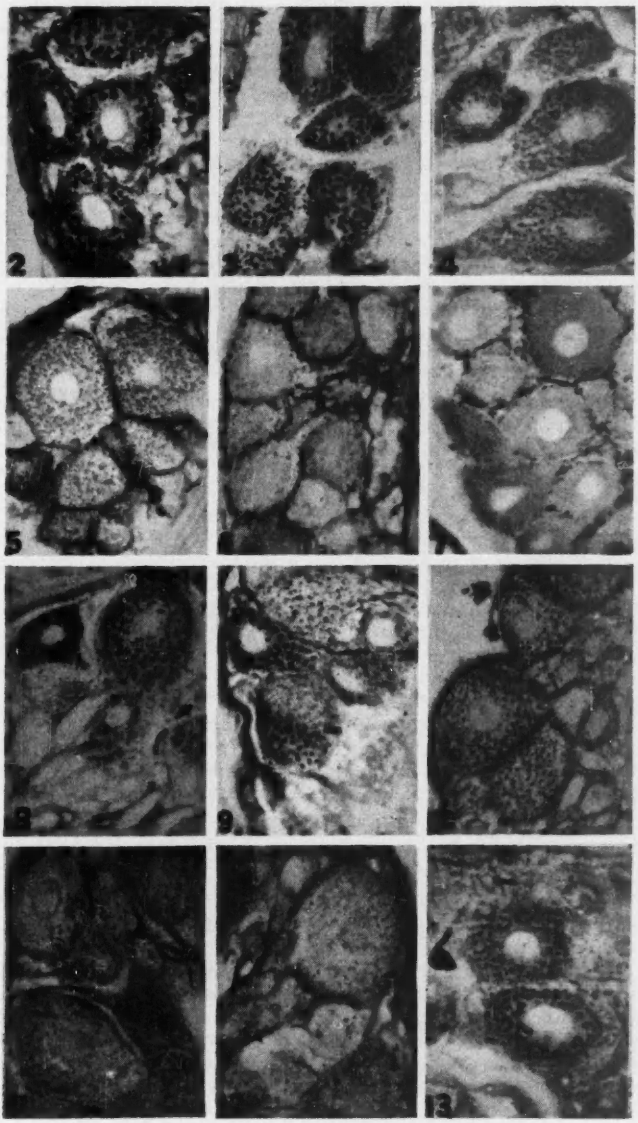
[4]Because of the similarities of the Golgi bodies in the normal and treated specimens between American cockroach and honeybee, the photomicrographic results of honeybee are omitted.

EXPLANATION OF PLATE I

FIG. 2. Normal condition.

FIGS. 3–7. DDT-treated specimens: 3, Knockdown stage, with normal looking Golgi bodies; 4, a typical breaking up of the Golgi bodies in knockdown stage; 5–6, Successive stages in morbid cockroaches; 7, Dead stage.

FIGS. 8–13. BHC-treated specimens: 8, Knockdown stage; 9–10, successive stages in morbid cockroaches (note 9, some cells with broken Golgi bodies, one cell with normal-looking Golgi bodies, one cell with half full of normal Golgi bodies and the other half full of broken ones); 11–13, different conditions in dead cockroaches.



Golgi bodies in ganglionic cells of *Periplaneta americana* (L.).

ring, pear, short filament, and many other irregular shapes. However, they are more or less rounded. They are well developed in active stages of differentiation and become less and less conspicuous as the cell ages. In some resting old cells, we find no Golgi bodies in the cytoplasm.

In the honeybee, the Golgi bodies look the same as in the cockroach, only they are somewhat smaller and not so abundant.

2. *Structure of the Golgi Bodies in Treated Ganglionic Cells*

Knockdown Specimens. With DDT (Figs. 3, 4) treatment, in both cockroaches and honeybees, the Golgi bodies in the active cells begin to break up. In appearance, they seem less smooth than in the normal condition. Generally, they are still large and conspicuous; in a few cases they resemble the normal condition (Fig. 3).

With BHC treatment, in bees and cockroaches, in most cases, the Golgi bodies remain the same as in the normal condition. In a few cases, the Golgi bodies may appear less coarse. Figure 8 shows both of the conditions in a BHC knockdown roach.

Morbid Specimens. In both bees and cockroaches, the Golgi bodies are further broken up with DDT treatment (figs. 5, 6). The granules become finer and finer, and, in some cases, even become so inconspicuous that they disappear almost entirely (Fig. 6). Usually, the breaking of the Golgi bodies in bees is not so prominent as in cockroaches.

With BHC treatment, the Golgi bodies start to break up. Some of them remain in a more or less normal condition. Figure 10 shows a typical condition of this stage. It is interesting to note, as shown in fig. 9, that there are some cells with broken Golgi bodies, one cell with normal Golgi bodies, one cell with one part full of normal-looking Golgi bodies and the other part full of broken ones. This shows how the Golgi bodies undergo a process of breaking up. The same condition occurs in both cockroaches and honeybees.

Dead Specimens. With DDT treatment, in the cockroach (fig. 7), the Golgi bodies undergo a complete breaking up. They either become very fine particles or entirely disappear. In the bees the Golgi bodies appear similar to those in the cockroach, except that we can usually find some very fine particles of the Golgi bodies in their cells.

With BHC treatment (figs. 11, 12, 13), in the dead bees and cockroaches, we can still see fine, even rather conspicuous, definitely identifiable Golgi bodies. We have never found this condition in DDT-killed bees and cockroaches.

DISCUSSION AND CONCLUSION

Cowdry (1924) found, that in pathologically or physiologically abnormal tissue, the Golgi bodies may show remarkable alterations. He listed the alterations reported by many observers, such as Monti, Cajal, Da Fano, Cowdry, and others. The alterations reported are chiefly fragmentation, pulverization and disappearance, reduction in size, condensation, hypertrophy followed by disintegration, and migration or change in position. In nerve cells, Cajal (1914) reported fragmentation, pulverization, and migration of Golgi bodies in pathological conditions. When Da Fano (1921) exposed white rats to cold,

he noticed hypertrophy followed by disintegration of Golgi bodies in nerve cells. Battistessa reported reduction in size and condensation of Golgi bodies in nerve cells after lead and strychnine poisoning, but no tendency to dispersal (Cowdry 1924). These investigators proved that the Golgi bodies may break up, or fragmentate in the nerve cells in the pathological condition. The author has reached the same conclusion in this work. In honeybees and American cockroaches which were killed by DDT or BHC, the Golgi bodies usually break up and finally disappear. The successive stages of breaking up are illustrated in fig. 1.

The classification of the treated specimens into three groups, knockdown, morbid, and dead, is an artificial one set up for the benefit of preparation and observation. Actually, there is no sharp division among these groups. Therefore, in the final results, the condition of one group may also exist in others. Other factors, in addition to this artificial classification, such as the variation of the time of treatment of individuals, the difference in physiological condition of individuals, and the various differentiating stages of the cells, could also produce a lack of uniformity in the results. However, in all cases, the course of the breaking up of the Golgi bodies is traceable.

In the normal ganglia of the cockroach, we may occasionally find some Golgi bodies which resemble a typical DDT-knockdown condition. This may be due to a physiological abnormality of the cockroach, or to the age of the ganglionic cells, or to some unknown factor. Figure 3 shows some Golgi bodies in normal condition in a DDT-knockdown cockroach. This may be due to a too early fixation of the specimen or to other reasons. In the cockroach, there are a group of cells, located in the ganglion between the two longitudinal connective nerves (fig. 13), which usually are not very sensitive to DDT or BHC. The Golgi bodies in these cells are rather hard to break up. The reason for this phenomenon is unknown to the author. In the bee, the change of the Golgi bodies is usually not as significant as that in the cockroach. The reason may be that the bee is much more sensitive to DDT or BHC than is the cockroach. The bees always die within several hours following treatment, while the cockroaches can keep alive for several days. In such a short time, the Golgi bodies in the bees may not be able to change as fast as in the cockroaches. The bees used in this study were all adults whose ganglionic cells are mostly resting cells, or cells in less differentiating stages; while the cockroaches are all last nymphal instars whose ganglionic cells are mostly in an active differentiating stage. Therefore, we find less active cells with prominent Golgi bodies in either normal or treated bees than in cockroaches.

To sum up, generally speaking, in the DDT treated specimens, the Golgi bodies begin to break up prominently in the knockdown group; then the Golgi bodies become less and less conspicuous and even vanish as the insects become morbid and die. In the BHC treated specimens, the Golgi bodies undergo the same course of breaking up, except that they remain fairly normal in the knockdown stage, and can still be identified in the dead stage. These facts tend to show that DDT has a tendency to speed up the breakage of the Golgi bodies in the nerve cell of insects, while BHC has no such effect.

SUMMARY

The mode of action of DDT is still questionable; however, we do know that it affects the nervous system, as well as the metabolism and the physiological mechanism of the insects. The gamma isomer of BHC is not a nerve poison and is highly toxic to insects. Therefore, it was used as a check treatment in comparison with DDT to show the significance of the results.

American cockroaches, representing a primitive insect, and honeybees, representing a highly specialized insect, were the materials used in this study. The thoracic ganglia of the last nymphal instar cockroaches and of the honeybees, and the last abdominal ganglion of cockroaches were dissected out and fixed and impregnated according to the silver method devised by Da Fano.

In both DDT and BHC treatments, the treated specimens were divided into three groups, knockdown, morbid, and dead, for observation.

In BHC-treated specimens, the Golgi bodies underwent a rather usual process of breaking up; while in DDT-treated specimens, the Golgi bodies mostly started to break up early in the knockdown stage, and almost vanished in dead ones. Therefore, DDT seems to have an effect on insect ganglionic cells which speeds up the breakage of the Golgi bodies.

LITERATURE CITED

Bodenstein, Dietrich. 1946. Investigation on the locus of action of DDT in flies (Drosophila). Biol. Bull., 90(2): 148–157.

Bourne, G. 1942. Cytology and cell physiology. Oxford Univ. Press, London. 296 pp.

Bowen, R. H. 1924. On a possible relation between the Golgi apparatus and secretory products. Amer. Jour. Anat., 33: 197–217.

1926. The Goldi apparatus—its structure and functional significance. Anat. Record, 32: 151–193.

Bozkurt, Bedia. 1948. Vergleichende Untersuchungen zur Aufnahme von Insekticiden (DDT und Gammexane) in den Arthropodenkorper. Istanbul Univ. Fen Fakultesi Mecmuasi (Rev. Fac. Sci. Univ. Istanbul) Ser. B. Sci. Nat., 13(1): 55–56.

Brice, A. T., R. P. Jones, and **J. D. Smyth.** 1946. Golgi bodies by phase contrast microscopy. Nature, 157(3991): 553–554.

Buston, H. W., S. E. Jacobs, and **A. Goldstein.** 1946. (Note on the physiological activity of gammexane.) Nature, 158(4001): 22.

Cajal, S. R. 1914. Algunas variaciones fisiologicas y patologicas del aparato reticular de Golgi. Trab. Lab. Inv. Biol., 12: 127–227.

Campbell, F. L. 1946. The action of insecticides. Sci. Month., 63(2): 153–156.

Carleton, H. M. 1919. Notes on Cajal's formalin-silver nitrate impregnation method for the Golgi apparatus. Jour. Roy. Micr. Soc., pp. 321–328.

Carey, R. J., E. M. Downer, F. B. Toomey, and **E. Haushalter.** 1946. Morphological effects of DDT on nerve endings, neurosomes and fiber types in voluntary muscles. Proc. Soc. Exp. Biol. Med., 62: 76–83.

Cowdry, E. V. 1922. The reticular material as an indicator of physiologic reversal in secretory polarity in the thyroid cells of the guinea pig. Amer. Jour. Anat., 30: 26–37.

1923. The significance of the internal reticular apparatus of Golgi in cellular physiology. Science, 58: 1–7.

1924. General cytology. Univ. Chicago Press. 754 pp.

Da Fano, C. 1920. Method for the demonstration of the Golgi apparatus in nervous and other tissues. Jour. Roy. Micro. Soc., pp. 157–161.

1921. Changes in Golgi's apparatus in nerve cells of the spinal cord following exposure to cold. Jour. Nerv. Ment. Dis., 53: 353–360.

Deane, H. W., and **E. W. Dempsey.** 1945. The localization of phosphatases in the Golgi region of intestinal and other epithelial cells. Anat. Rec., 93: 401–417.

Draize, J. H., A. A. Nelson, and **H. O. Calvery.** 1945. Precutaneous absorption of DDT in laboratory animals. Jour. Pharm. Exp. Therap., 82: 159–166.

De Robertis, E. D. P., W. W. Nowinski, and **F. A. Saez.** 1948. General cytology. W. B. Saunders Co., Philadelphia. 345 pp.

Emmel, V. M. 1945. Alkaline phosphatase in the Golgi zone of absorbing cells of the small intestine. Anat. Rec., 91: 39–47.

Golgi, C. 1898. Sur la structure des cellules nervouses. Arch. Ital. Biol., 30: 60–71.

1898a. Sur la structure des cellules nervouses des ganglions spinaux. Arch. Ital Biol., 30: 278–286.

Hartzell, Albert. 1945. Histological effects of certain sprays and activators on the nerves and muscles of the housefly. Contr. Boyce Thompson Inst., 13(9): 443–454.

Hayes, W. P., and **Yu-Su Liu.** 1947. Tarsal chemoreceptors of the housefly and their possible relation to DDT toxicity. Ann. Ent. Soc. Amer., 40: 401–416.

Kirkman, H., and **A. E. Severinghaus.** 1938. A review of the Golgi apparatus. Anat. Rec., 70: 413–431; 70: 557–573; 71: 79–103.

Kirkwood, S., and **P. H. Phillips.** 1946. The anti-inositol effect of gamma hexachlorocyclohexane. Jour. Biol. Chem., 163: 251–254.

Lee, A. B. 1937. The microtomist's vade-mecum. P. Blackiston's Son & Co., Inc., Philadelphia. 784 pp.

Ludwig, D. 1946. Effect on DDT on the metabolism of Japanese beetle. Ann. Ent. Soc. Amer., 39: 496–509.

McClung, C. E. 1937. Handbook of microscopical technique. P. B. Hoeber, Inc., New York. 698 pp.

McNamara, B. P., and **S. Krop.** 1948. Observation on the pharmacology of the isomers of hexachlorocyclohexane. Jour. Pharm. Exp. Therap., 92: 140–146.

1948a. The treatment of acute poisoning produced by gamma hexachlorocyclohexane. Jour. Pharm. Exp. Therap., 92: 147–152.

1949. The influence of delta and gamma benzene hexachloride upon the oxygen uptake of the brain. Science, 109(2831): 330–331.

Nassonow, D. N. 1923. Das Golgische Binnemetz und seine Beziechungen zur der Sekretion. Arch. f. Mikr. Anat. u. Ent., 97: 136–186.

Nelson, A. A., J. H. Draize, G. Woodward, O. G. Fitzhugh, R. B. Smith, Jr., and **H. O. Calvery.** 1944. Histopathological changes following administration of DDT to several species of animals. (U. S.) Public Health Reports, 59(31): 1009–1020.

Philips, F. S., A. Gilman, and **F. N. Crescitelli.** 1946. Studies on the pharmacology of DDT. II. The sensitization of the myocardium to sympathetic stimulation during acute DDT intoxication. Jour. Pharm. Exp. Therap., 86: 222–228.

Reiss, P. 1922. L'appareil de Golgi dans les cellules glandulaires de l'hypophyse polarite fonctionelle et cycle secretoire. Compt. Rend. Soc. Biol., Paris, 87: 255–256.

Richards, A. G., Jr., and **L. K. Cutkomp.** 1945. Neuropathology in insects. Jour. New York Ent. Soc., 53(4): 313–355.

1946. Correlation between the possession of a chitinous cuticle and sensitivity with DDT. Biol. Bull. 90(2): 97–108.

Ricker, W. F., V. R. Huebner, S. B. Raska, and **McK. Cattell.** 1946. Studies on 2, 2 bis (P-chlorophenyl)-1, 1, 1 trichloroethane (DDT): effects on oxidative metabolism. Jour. Pharm. Exp. Therap., 88: 327–332.

Roark, R. C., and **N. E. McIndoo.** 1947. A third digest of the literature on DDT. U. S. D. A. Bur. Ent. and Pl. Quar., E-728.

Roeder, K. D., and **E. A. Weiant.** 1946. The site of action of DDT in the cockroach. Science, 103(2671): 304–306.

Slade, R. E. 1945. The gamma isomer of hexachlorocyclohexane (gammexane). An insecticide with outstanding properties. Chem. and Ind., 64: 314–319. (London).

Snodgrass, R. E. 1925. Anatomy and physiology of the honeybee. McGraw-Hill Book Co., New York. 327 pp.

1935. Principles of insect morphology. McGraw-Hill Co., New York. 667 pp.

Tobias, J. M., and **J. J. Kollros.** 1946. Loci of action of DDT in the cockroach (*Periplaneta americana*). Biol. Bull., 91(3): 247–255.

Tobias, J. M., J. J. Kollros, and **J. Savit.** 1946a. Acetylcholine and related substances in cockroach, fly, and crayfish and the effect of DDT. Jour. Cell. and Comp. Physiol., 28(2): 159–182.

1946b. Relation of absorbability to comparative toxicity of DDT for insects and animals. Jour. Pharm. Exp. Therap., 86: 287–293.

Welsh, J. H., and **H. T. Gordon.** 1946. The action of DDT on crustacean nerve. Anat. Record, 96(4): 557.

1947. The mode of action of certain insecticides on the arthropod nerve axon. Jour. Cell. and Comp. Physiology, 30(2): 147–171.

Worley, L. G. 1946. The Golgi apparatus, an interpretation of its structure and significance. Ann. New York Acad. Sci., 47: 1–55.

Yeager, J. F., and **S. C. Munson.** 1945. Physiological evidence of a site of action of DDT in an insect. Science, 102: 305–307.

Zawarzin, A. 1924. Das Bauchmark der Inseckten. Ein Beitrag zur vergleichenden Histologie (Histologische Studied uber Insekten VI). Zeit. Wiss. Zool., 122: 323–424.

THE CHEMISTRY AND ACTION OF INSECTICIDES, by HAROLD H. SHEPARD. iii+504 pages, 111 tables, 22 figures. McGraw-Hill. Price, $7.00.

I had the very good fortune to take a course on insecticides under Dr. Shepard as a graduate student at the University of Minnesota in the middle 30's. No text could be assigned because there were none suitable. Fortunately, however, extensive mimeographed references were issued to his students as the course progressed. These references and lecture notes were highly prized since they represented the only current digest and source of literature on the latest developments in the field.

Dr. Shepard's earlier mimeographed work, "The Chemistry and Toxicology of Insecticides" (1939), which underwent eight or more printings, was a natural outgrowth of the assembled materials for this course. The present volume is a further outgrowth of it, but has undergone a drastic revision. Subjects under discussion include the inorganics containing arsenic, fluorine, sulfur, copper and a group of miscellaneous inorganic and metal-organic substances, the botanicals, the oils, synthetics, principles of chemical control of insects, the relative toxicity and mode of action of insecticides and finally a chapter on attractants and repellents. The literature is freely cited in the discussion and extensive papers are listed at the close of each chapter.

He has made an attempt to bring us up to date on the rapidly-changing field of insecticides. This book is well-written. It will become a popular college text as well as a valuable reference for professional people engaged in insect control.—H. S. TELFORD.

A CLASSIFICATION OF THE MUSCOID CALYPTRATE DIPTERA[1]

SELWYN S. ROBACK
University of Illinois,
Urbana, Illinois

The objective of this study was to see if a coordinated study of both adults and larvae of the calyptrate Diptera would bring out any new relationships within the group. With this objective in mind, larvae of all groups were examined, or descriptions gleaned from the literature, to determine what characters they offered and what groupings they fell into on the basis of the characters found. The present day adult groupings were then re-examined and considered in relation to those offered by the larvae. The resultant classification is based on characters offered by both and has involved a shifting in rank of some groups formerly based only on adult characters.

In the past, the larvae have not been used to any great extent in the classification of the calyptrate muscoids. Townsend (1935–42) is one of the few to make use of larvae in the classification of the calyptrates. Hall (1947) has used larvae in the Calliphoridae. Most of the work that has been done concerned chiefly species of medical or economic importance. At present non-economic species are very incompletely known and many are not associated with their corresponding adults.

The results of this study are of a preliminary nature, and indicate the need for consideration of a great deal more material than is now available. Even so, results obtained do illustrate the great value of larval characters in a consideration of the phylogeny of the group. It is hoped that they will help to stimulate the rearings and preservation of more larval forms. It is believed that through a thorough knowledge of the larvae, a better understanding of the relationships within the calyptrate muscoids will be achieved.

In this study the Muscoidea and Sarcophagoidea are treated in some detail and the Oestroidea are considered only briefly, because of the small number of larvae available.

ACKNOWLEDGMENTS

The writer should like to express his appreciation and gratitude to Dr. Herbert H. Ross for his interest, cooperation, and constructive criticism during the preparation of this work.

I am also greatly indebted to Dr. Ross for putting the extensive collections of adult and larval Diptera of the Illinois Natural History Survey as well as its facilities, at my disposal. The donation of the larvae of *Atherigona* sp. by the U. S. National Museum, arranged

[1]A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Entomology in the Graduate School of the University of Illinois. This paper is a joint contribution from the Department of Entomology, University of Illinois, and the Illinois Natural History Survey, Urbana, Illinois.

by Mr. C. W. Sabrosky and the loan of slides of *Hydromyza confluens* Loew by Dr. H. Dietrich of Cornell University is here gratefully acknowledged.

To two of my fellow students, Edwin W. King and Robert Alrutz, thanks are due for their suggestions and cooperation.

HISTORICAL

The literature on the calyptrate muscoids is extremely large and scattered. In this paper it will not be possible to do more than touch the highlights.

Any history of this group must start with Linnaeus (1758). In his classification of the Diptera most of the calyptrates were contained in his "genera" *Musca*, *Oestrus* and *Conops*. After his time, many workers, such as Meigen (1800 and 1803), Latreille (1805), Robineau-Desvoidy (1830), Macquart (1834), Westwood (1840), Osten-Sacken (1884) and many others did work in this group. As they added more and more characters to those known at Linnaeus' time, the concept of families and genera within the calyptrates became clearer and better defined.

In 1893 Girschner culminated this progression with a classification which more nearly approached our modern ideas than any previous attempt. Using a wide variety of characters, he divided the calyptrates into the "Anthomyiden" and "Tachiniden." The "Anthomyiden" correspond roughly to the Muscoidea of this paper, while the "Tachiniden" correspond to the Oestroidea plus the Sarcophagoidea. The Cordyluridae are included in his Calyptratae.

The next major work, including a comprehensive treatment of the calyptrate muscoids, was that of Williston (1908). In his account of the North American Diptera, he divides the Calyptratae into six families. The Oestridae, Tachinidae (including the Miltogramminae), Sarcophagidae and Dexiidae, correspond generally to Girschner's "Tachiniden." Williston, however, included most of the Calliphoridae in his family Muscidae. This latter, plus the Anthomyiidae, equal Grischner's "Anthomyiden." The Cordyluridae are included in the Acalyptratae. After Williston, many workers, such as Parker (1914 and 1919), Aldrich (1916), Malloch (1917–23), Shannon (1923–26), Séguy (1923 and 1937), Allen (1926) and Townsend (1892 and 1914) worked on various groups within the calyptrates or on the Calyptratae as a whole. They added more characters at all levels and published specific revisions of the families and subfamilies.

Curran, in 1934, published a new comprehensive account of the North American Diptera. In this, he lumps the Scatophagidae (Cordyluridae), the Anthomyiidae, and those Muscidae of Williston's manual which lack hypopleural bristles, with the Muscidae. The Sarcophagidae (including the Miltogramminae), a few Tachinidae, and those Muscidea of Williston's manual with hypopleural bristles (Calliphoridae) are included in the Metopiidae. The Tachinidae, Oestridae and Cuterebridae are separate families. Townsend (1935–42) gave a comprehensive treatment of some Calyptrate groups but his work is difficult to use.

This outline, though brief, gives the major steps in the classification

of the calyptrate muscoids and offers a basis for comparison with the classification here proposed.

In this paper the Meigen 1800 names will be used in place of the 1803 names which have been more commonly used in the United States. The changes involved are:

Scopeuma in place of *Scatophaga*.
Scopeumatinae in place of Scatophaginae.
Larvaevoridae in place of Tachinidae.

LIMITATIONS AND MATERIALS

The keys included in this paper are applicable only to the North American fauna. The Old World groups Eginiinae and Glossinidae, which have no representative in North America, are not included.

The adult material and most of the larval material used came from the collection of the Illinois Natural History Survey.

When good larval descriptions accompanied by figures were to be found in the literature, these were incorporated into this study. Credits are given with the figures. The number of genera of adults and larvae used in making up the descriptions is noted at the beginning of each subfamily description.

PREPARATION OF MATERIALS

In order to study properly the buccal armature and posterior spiracles of muscoid larvae, some special preparations are necessary.

The buccal armature is normally surrounded by layers of fat and muscle, only the tips of the oral hooks being visible externally. If the larva has a smooth, thin skin, piercing it in one of the posterior segments to prevent collapse and the running it through an alcohol series into xylene and then into clove oil, will often show the buccal armature in sufficient detail for study. When this is not feasible, there are two alternatives recommended.

The first method is to cut off the anterior part of the body containing the buccal armature and clear it in a strong solution of cold potassium hydroxide (about 15–25%). The time required for clearing will vary with different specimens. These must be kept under observation during this process. When the material is judged to be sufficiently cleared, it can be removed to distilled water and the liquified muscle and fat gently squeezed out or removed with a fine pipette. This will leave the buccal armature clearly visible in place. Seventy percent alcohol is adequate for study and storage.

The second method is carefully to dissect out the buccal armature, removing as much of the fat and muscle as is feasible without damaging the armature. Then the specimen is run through an alcohol series into xylene and finally cleared in clove oil. Though much shorter than the previous method, this process is slightly more difficult and does not show the buccal armature in relation to the body segments. On the other hand, if carefully done, it avoids the danger of loss of fine parts and the distortion of the relative sclerotization which may result from excessive treatment with potassium hydroxide.

For cursory study, the posterior spiracles can be observed directly on the specimen. For more detailed observation, however, they are

best prepared by carefully cutting them out of the posterior plate and, after proper dehydration, mounting them in balsam on a microscope slide. In old larvae, the spiracular plates may be extremely opaque and a light treatment with potassium hydroxide may be necessary to render the spiracular openings clearly visible.

The adults and the remaining larval characters require no special preparation for observation.

MORPHOLOGY AND TERMINOLOGY

In general, the morphological characters used in the keys to adults and descriptions of adults are well known and can be found in most standard reference works and glossaries. The intrapostocular cilia have not been used much in the past. They are a row of fine hairs located between the hind margin of the eye and the first row of postocular bristles. Fairly high magnification is required in order to see them. The other adult characters will not be repeated here.

The larval characters are not so well known and, in view of the importance here ascribed to them, will be gone into in some detail.

Externally the third instar larva, fig. 86, is divided into twelve segments. The first of these, through which the oral hooks protrude, is bilobed and called the pseudocephalon (pcn). Behind this are the three thoracic segments (It-IIIt), followed by eight abdominal segments (1-8). Anteriorly and ventrally many of the thoracic and abdominal segments bear patches of spines, called ventral spine bands (vsb), fig. 98. The posterior end of the eighth abdominal segment is generally flattened or slightly rounded and is called the posterior plate (pp), fig. 39. This plate may have a ring of circumspiracular palpillae (csp) around its periphery, or a cavity in its center (pc) or both, figs. 39 and 45. The anal plate and anal papillae (ap) lie below the posterior plate, fig. 39.

The buccal armature, fig. 1, is located internally in the first few body segments. The oral hooks (oh) project from the pseudocephalon and are the only part of the armature visible externally. They are a paired structure, though they may be appressed so as to appear as a single median hook, fig. 36. In general, they are separate, slightly curved and pointed. They may also be toothed, fig. 6. Around the tips of the hooks, accessory sclerites (acs), fig. 8, may be present. These are very variable in form. Below the bases of the hooks, dental sclerites (ds) are almost always present. Basally the oral hooks articulate with the hypostomal sclerite (hs). This structure consists of two short longitudinal plates connected, ventrally and just ahead of their center, by a cross bar. In dorsal view it appears as an H. In turn, the hypostomal sclerite articulates with the pharyngeal sclerite (ps), fig. 1. This is a large trough-like structure prolonged, in lateral view, into two lobes with the pharyngeal groove (pg) between them. The lobes are called cornua, and are paired, fig. 36. The dorsal cornua (dcn) are generally separate, while the ventral cornua (vcn) are connected by the lower wall of the pharynx, fig. 36. Each of the cornua may have a clear window-like area, subterminally (dw and vw). The dorsal window (dw) may appear as a deep incision, fig. 33. Extending forward from the main body of the pharyngeal sclerite, one on each side, are the parastomal bars (pb), fig. 1. They are rod-like, sometimes detached

basally, and lie above the arms of the hypostomal sclerite. The oral hooks and the hypostomal sclerite may be fused, fig. 37, or the hypostomal sclerite and pharyngeal sclerite, fig. 2, but this is not common.

The anterior spiracles (asp) are located laterally at or before the intersegmental border of the first and second thoracic segments. Each spiracle is hand-like in shape or it may be sunken and appear externally as a pit.

The posterior spiracular plates (psp), fig. 51, are ovoid or reniform, and are located slightly above center in the posterior plate, fig. 39. They are generally separated and are in the posterior cavity if there is one. Delimiting each spiracular plate is a sclerotized rim called the peritreme (p), fig. 51. This may be open, fig. 85, or closed, fig. 70. Inside the peritreme are a number of openings of varying shape called the posterior spiracular slits (pss). A scar called the button (b) is located in each posterior spiracular plate. It may be centered but is generally toward the inner edge of the plate. In many forms it is vestigial or absent, fig. 85. The posterior spiracular plates may also be raised on spiracular stalks (ss), fig. 88.

PHYLOGENY

The calyptrate muscoids have undoubtedly originated from an ancestral acalyptrate stock. The morphological evidence seems to indicate that they are monophyletic and that the point of their departure was from otitid or helomyzid-like forms. The extant Otitidae and Helomyzidae have a combination of characters which could most nearly have given rise to those of the calyptrate muscoids. Both of these families have a rather complete venation and retain subcosta. Also most forms here have the sixth vein complete and reaching the wing margin. The last two characters are important in allying them to the calyptrate muscoids, in particular the Anthomyiidae. Oral vibrissae present in the Helomyzidae are lacking in the Otitidae.

Upon consideration of these families and the more primitive calyptrate muscoids a prototype with the following important characters can be postulated.

Adult

1. Wings retaining subcosta.
2. Sixth vein reaching wing margin.
3. Fourth vein ending behind wing tip.
4. No or only one sternopleural bristle.
5. Hypopleuron bare.
6. Mesothoracic postnotum not developed.
7. Arista bare.
8. Oral vibrissae weak if present.

Larva

1. Oral hooks separate.
2. Parastomal bars present.
3. Dorsal window present.
4. Posterior spiracular plates with three ovoid slits.
5. Food habits, saprophagous.

Of all the calyptrate muscoids the Anthomyiidae have diverged least from this prototype, and on this basis are considered the most primitive. The above list will fit the subfamily Scopeumatinae almost without change. Adult Anthomyiinae and a very few Scopeumatinae have added one or two sternopleurals and the arista is variable. In the larvae there is a tendency for loss of the parastomal bars and they have developed coprophagous and phytophagous nutrition.

From the ancestral Anthomyiidae three lines have diverged. In the first, represented by the Fanniidae and Muscidae, the sixth vein no longer reaches the wing margin, but the hypopleuron has remained bare. The larvae of *Fannia* are coprophagous and saprophagous and have lost the windows and parastomal bars. Following the loss of the windows and parastomal bars the oral hooks, in the Muscidae, have become appressed. In the more primitive forms which are carnivorous they are still individually movable. Eventually complete fusion, asymmetry, and spatulation have taken place and these larvae have gone into coprophagous and saprophagous nutrition. Adult Muscidae have up to four sternopleurals and the fourth vein sometimes ends before the wing tip.

The Sarcophagidae and Calliphoridae represent a second line of development. Here the hypopleuron is bristled and the fourth vein always ends before the wing tip in the adult. In the larvae the parastomal bars are retained and the oral hooks remain separate. The dorsal window, retained in the Sarcophagidae, is lost in the Calliphoridae. The larvae have become parasitic in insects and obligate and facultative animal parasites.

The Larvaevoridae and Oestridae, with the development of the mesothoracic postnotum, represent a third line. The hypopleuron is bristled as in the previous line. Larval morphology is extremely variable. Parastomal bars and windows are not present. Both families are wholly parasitic as larvae, the Larvaevoridae on insects and the Oestridae in mammals.

In this paper the Calyptratae are divided into three superfamilies, the Muscoidea, and Sarcophagoidea, and the Oestroidea, as outlined in the following synopsis and illustrated in text figure 1.

SYNOPSIS OF MAJOR DIVISIONS

Adults

1. Second antennal segment without laterodorsal longitudinal seam; thorax without complete transverse suture on dorsum, anterior to wings; abdominal spiracles one to five generally in membrane; subcostal vein often incomplete or imperfect; lower calypter normally undeveloped (not treated herein) ..... **ACALYPTRATAE**
   Second antennal segment with laterodorsal longitudinal seam; thorax normally with a complete transverse suture on dorsum, anterior to wings; abdominal spiracles normally in tergites; lower calypter usually large. ..... **CALYPTRATAE**—2
2. Either mesothoracic postnotum strongly biconvex or mouthparts greatly reduced; edges of abdominal sternites usually overlapped and at least partially hidden by margins of tergites, fig. 124 ..... **Oestroidea**
   Mesothoracic postnotum not prominent; first abdominal sternite overlaps margins of tergites, figs 125, 126 3
3. Hypopleuron bare or with weak hair; pteropleuron lightly pilose or bare ..... **Muscoidea**
   Hypopleuron with one or more rows of bristles below metathoracic spiracle; pteropleuron setose ..... **Sarcophagoidea**

Larvae (Third Instar)

1. Pharyngeal sclerite not well developed, generally weakly pigmented; either dorsal or ventral cornua may be narrow or almost absent; hypostomal sclerite often elongate; oral hooks separated; posterior spiracles variable, often on very long projections.....**ACALYPTRATAE**

   Pharyngeal sclerite well developed, generally well pigmented and robust, figs. 1 to 35; hypostomal sclerite generally short and robust; oral hooks separate or appressed; posterior spiracles plate-like, ovoid or reniform, with variable openings, figs. 51 to 85; at most are raised on short projections.....**CALYPTRATAE**—2

2. Pharyngeal sclerite either heavily pigmented, without windows or parastomal bars, cornua widely diverging or highly modified, figs. 37, 38; or cornua non-pigmented, large, figs. 34, 35; posterior spiracular plates ovoid or reniform, with slits or many closely packed small openings; parasitic on insects or mammals.....**Oestroidea**

   Pharyngeal sclerite moderately pigmented, often with windows and parastomal bars; never diverging as above, figs. 1 to 33; posterior spiracles never with more than 3 slits, figs. 51 to 85; mostly saprophagous or phytophagous, a few predaceous or parasitic..... 3

3. Posterior spiracular slits linear as in figs. 51 to 63 and 58 to 60, sinuate, as in figs. 54, 55, 61, 62, and 81 or short ovoid, fig. 82; lowest slit or lowest two slits generally slant lateroventrally from button; peritreme generally complete and button present; posterior spiracular plates never in depression, may be raised on stalks; oral hooks fused, fig. 36, or separate; parastomal bars may be present.....**Muscoidea**

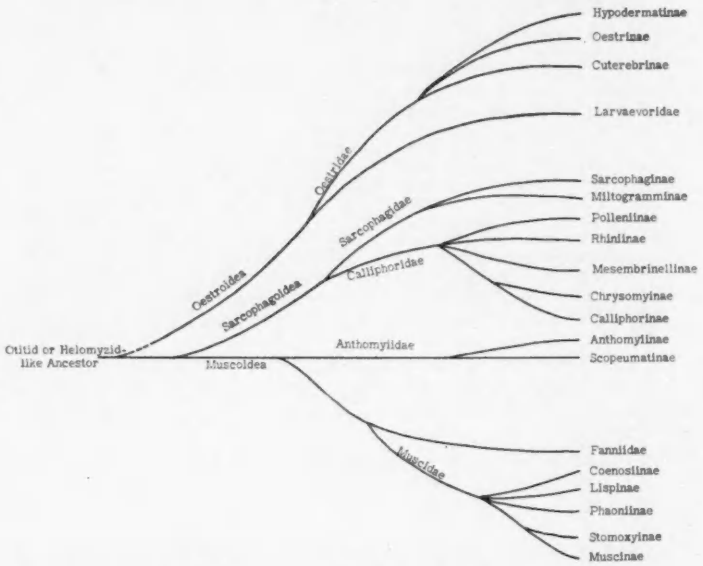
   Posterior spiracular slits linear as in figs. 69 to 71 and 76 to 78, never sinuate or short ovoid; lowest slits never slant lateroventrally from button; peritreme may be open, as in figs. 56, 64, 71, 78, and 83; posterior spiracular plates generally in depression, figs. 42, 45, 46, 49 and 50, never raised on stalks; oral hooks separate; parastomal bars generally present, figs. 24 to 33.....**Sarcophagoidea**

The above synopsis shows the characters and relationships of the larger groupings within the Calyptratae as well as the relationship between the Calyptratae and Acalyptratae. It is not a key for identification of specimens.

The Muscoidea contains, along with the Muscidae and Fanniidae, what is undoubtedly the most primitive calyptrate family, the Anthomyiidae. In this family the calypteres are small and equal in size.

Included in the Anthomyiidae is the subfamily Scopeumatinae. This group has been considered as a family by many writers, but its closest affinities are with the subfamily Anthomyiinae of most authors, and a good family separation between the two is lacking. These two subfamilies here comprise the family Anthomyiidae. In both groups the sixth wing vein reaches the hind margin of the wing, figs. 103, 110, while the larva of *Scopeuma stercorarium* Linn., which was examined, is distinctly anthomyoid in all its characteristics. It possesses the windows and flaring of the cornua, fig. 1, the tubercles on the posterior plate, fig. 39, the typical anthomyoid posterior spiracles, fig. 51, and the general body form of most anthomyiid larvae. From what material was available, it was evident that the genera commonly included in the Scopeumatinae are not an entirely homogeneous group. The buccal armature of *Hydromyza confluens* Loew, fig. 2, though it is a specialized form, lacks windows in the cornua and shows many acalyptrate characteristics. Crampton (1944) has pointed out that the male genitalia of the genera *Parallelomma* and *Scopeuma*, both included in the Scopeu-

matinae, are quite distinct and could have been derived from different sources in the Acalyptratae. If the evidence of the male genitalia is reliable, the Anthomyiinae developed from the line of ***Scopeuma*** rather than ***Parallelomma***. Larvae of the Scopeumatinae are very poorly known and it is believed that the rearing of more of them would do much to clear up the relationships in this subfamily. The presence of three or four sternopleural bristles and fine hairs on the undersurface of the scutellum, fig. 119, will separate most of the members of the Anthomyiinae from the Scopeumatinae.



TEXT FIG. 1. A phylogenetic tree of the calyptrate muscoid Diptera.

On the basis of the male genitalia, and the presence of the three sternopleurals the Anthomyiinae can be considered more advanced than the Scopeumatinae, and closer to the remainder of the Muscoidea and the Sarcophagoidea. It is from the progenitors of the Anthomyiidae that the Fanniidae, Muscidae and the Sarcophagoidea probably arose.

The larvae of the Sarcophagoidea and Anthomyiidae have many characters in common. The vertical flaring of the pharyngeal sclerite, the windows, separate oral hooks, figs. 23 to 33 and 3 to 6, and the tubercles on the posterior plate, figs. 36, 49, and 39, 47, are present generally in both groups. The parastomal bars, present in all the Sarcophagoidea, figs. 23 to 33, are present in some Anthomyiidae, figs. 3 to 5, and absent in others, fig. 6. This fact undoubtedly indicates that the ancestral Sarcophagoidea separated from some early

Anthomyiidae before the tendency to loss of the parastomal bars appeared within that group. The male genitalia, particularly those of the Calliphoridae, also indicate a close relationship between the Anthomyiidae and the Sarcophagoidea. The presence of hypopleural bristles in the adults of the Sarcophagoidea has been used to link them to the Oestroidea. The larval characters, however, indicate that this character has been overrated and that the Sarcophagoidea are in reality much closer to the Muscoidea.

It is not so easy to derive the Muscidae directly from the Anthomyoid stock. In fact, were it not for an intermediate group such as the Fanniidae the gap would be quite difficult to span. As has been previously noted, in the larval Anthomyiidae the mouth hooks are separate, the cornua flare and have windows, and parastomal bars are generally present, figs. 3 to 6. In the Muscidae the oral hooks are appressed, fig. 36, the cornua generally do not flare and do not have windows, figs. 8 to 22, and there are never parastomal bars. Between these two extremes is ***Fannia*** in which the oral hooks are still separate, but the cornua do not flare and do not have windows, and there are no parastomal bars, fig. 7. It is undoubtedly a step in the transition from the Anthomyiidae to the Muscidae. The external form of ***Fannia***, fig. 102, is highly adaptive and of little use in tracing such characters as the posterior spiracles and the tubercles of the posterior plate. The posterior spiracles of the subfamily Phaoniinae, figs. 53, 60, 66, 73, and 80, of the Muscidae greatly resemble those of the Anthomyiidae, figs. 52, 58, 59, 65, 72, and 79, and the tubercles of the posterior plate are retained, though in reduced form, in ***Synthesiomyia nudiseta*** Van der Wulp, fig. 40. Besides the buccal armature the male genitalia also indicate an intermediate position for ***Fannia***. As Crampton (1944) has pointed out, ***Fannia*** could be placed in either the Muscidae or the Anthomyiidae and is closely related to both.

The family Muscidae can be defined by the condition of the larval oral hooks. In all the larvae of this group, either examined or known to me, the oral hooks are fused or so appressed as to appear fused, fig. 36. This will separate them from any other calyptrate group. In the adult stage the sixth vein does not reach the wing margin nor does the seventh vein curve toward it, figs. 105–107, 111 to 113, and 115. These characters will separate the Muscidae from the Anthomyiidae and the Fannidae respectively.

The subfamily limits within the Muscidae have been subject to much shifting. This is in a large part due to the existence of intergrades. In any set of groupings of the Muscidae there are always a few genera which will fall in between the groups chosen. Huckett (1936) has treated such a group of genera. Another result of the presence of these intergrades in that a combination of characters is required to separate the adult Muscidae into any groupings. The larvae on the other hand show much more clear cut differences, particularly in the arrangement of the posterior spiracular slits. The Phaoniinae are characterized by three elongate ovoid slits which radiate from the button such as in figs. 60 and 67. Included in this subfamily are the members of the genus ***Limnophora*** whose aberrant external form, figs. 88, 89, and 96, is undoubtedly adaptive to their aquatic environment. They do not

merit subfamily distinction on this basis. Their posterior spiracles are also typically phaoniine, fig. 53. In the Muscinae the slits are highly sinuate and arranged in an arc or circle to one side of the button, such as in figs. 54, and 81. In the Stomoxyinae the slits are also sinuate, but they are shorter and surround the button, figs. 55 and 62. The larval characters for the Lispinae and Coenosiinae are tentative. because of the fact that only one form was available for study in each. The adult groupings correlate with those of the larvae, but as was noted previously the separations are not so clear cut.

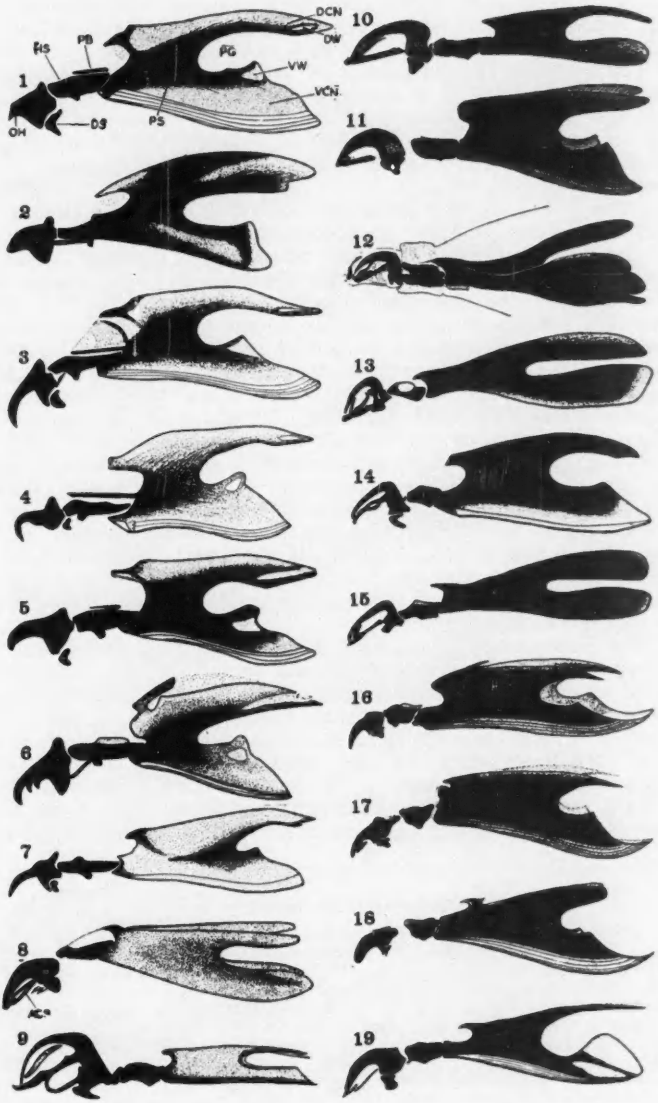
The genera previously placed in the Fanniinae are intermediate between the Anthomyiidae and the Muscidae. Some of the reasons for this statement have been discussed previously and will be repeated here. The larval oral hooks of the Fanniinae are separate in contrast to the appressed hooks of the Muscidae. The fanniine pharyngeal sclerite, fig. 7, lacks the flaring and windows of the cornua, and the parastomal bars of the Anthomyiidae, figs. 1 to 6. In the adult wings of the Fanniinae the sixth vein does not reach the wing margin as it does in the Anthomyiidae, figs. 103, 110. The seventh vein, however, curves towards the sixth so that if extended they would meet before the wing margin, fig. 104. This is in contrast to the almost parallel condition of these veins in the Muscidae, as shown in fig. 111. On the basis of the differences listed above it is obvious that the genera of the Fanniinae could not be satisfactorily included in either the Anthomyiidae or the Muscidae. It is therefore proposed that the subfamily Fanniinae be raised to family rank as the Fanniidae.

EXPLANATION OF PLATE I

Third instar larvae, buccal armatures: FIG. 1. *Scopeuma* sp. FIG. 2. *Hydromyza confluens* Loew. FIG. 3. *Paregle cinerella* Fall. FIG. 4. *Fucellia* sp. FIG. 5. *Hylemya antiqua* Meig. FIG. 6. *Pegomya hyoscyami* Panz. FIG. 7. *Fannia canicularis* Linn. FIG. 8. *Hebecnema umbratica* Meig. (after Thomson 1937). FIG. 9. *Phaonia variegata* Meig. (after Thomson 1937). FIG. 10. *Mydaea pagana* Fabr. (after Thomson 1937). FIG. 11. *Muscina pabulorum* Fall. (after Thomson 1937). FIG. 12. *Limnophora exurda* Pand. (after Tate 1939). FIG. 13. *Limnophora* (*Lispoides*) *aequifrons* Stein. FIG. 14. *Atherigona* sp. FIG. 15. *Lispe sociabilis* Loew. FIG. 16. *Orthellia cornicina* F. (after Thomson 1937). FIG. 17. *Dasyphora cyanella* Meig. (after Thomson 1937). FIG. 18. *Morellia simplex* Loew (after Thomson 1937). FIG. 19. *Polietes hirticrura* Meade (after Thomson 1937).

ABBREVIATIONS USED IN PLATES

acs—accessory sclerites
ap—anal papillae
asp—anterior spiracles
b—button
c—costa
csp—circumspiracular papillae
dcn—dorsal cornua
ds—dental sclerite
dw—dorsal window
hs—hypostomal sclerite
oh—oral hooks
p—peritreme
pb—parastomal bars
pc—posterior cavity
pcn—pseudocephalon
pg—pharyngeal groove
pp—posterior plate
ps—pharyngeal sclerite
psp—posterior spiracular plate
pss—posterior spiracular slit
sc—subcosta
ss—spiracular stalk
vcn—ventral cornua
vsb—ventral spine band
vsc—ventral scutellar hairs
vw—ventral window
1-8—larval abdominal segments
I-VII—longitudinal wing veins
It-IIIt—larval thoracic segments


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
DCN
DW
PG
VW
VCN
PS
PB
PS
OH
DS

The families Calliphoridae and Sarcophagidae here comprise the superfamily Sarcophagoidea. These two are extremely close and are included in one family by authors such as Curran (1934).

The presence of intrapostocular cilia in the Calliphoridae will serve to separate them from the Sarcophagidae. These are very fine and located between the rear margin of the eye and the first row of postocular cilia. Generally the dorsal cornua of the calliphorine larval pharyngeal sclerite lacks the deep incision present in the same structure in the Sarcophagidae.

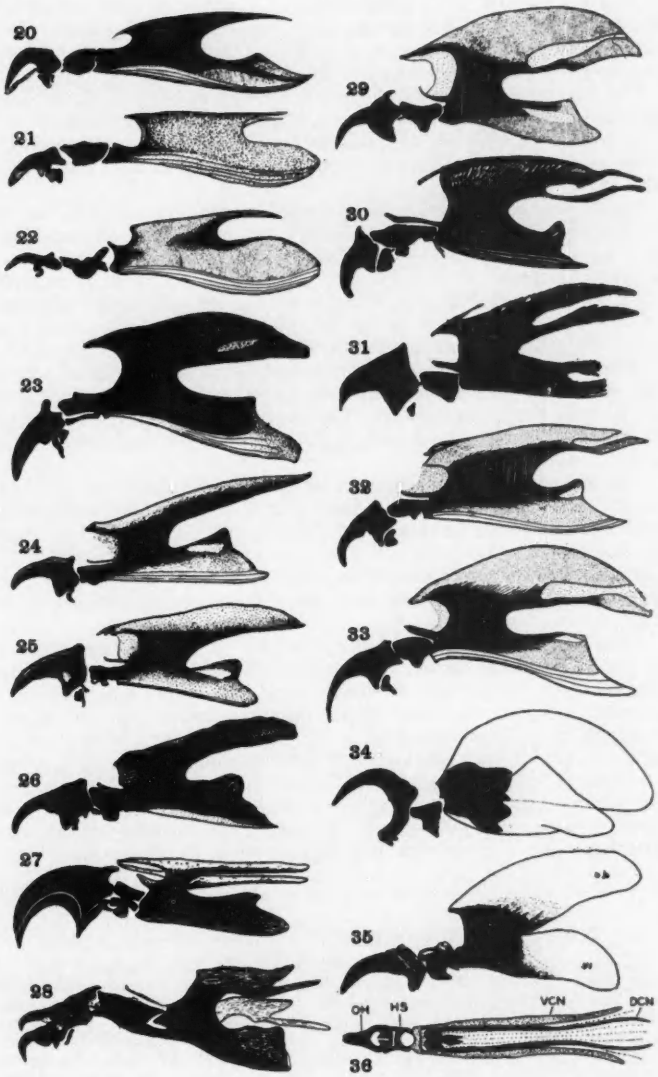
In the past the Calliphoridae have also been considered close to the Muscidae, Williston (1908) includes most of the calliphorid genera in his family Muscidae. There is little doubt however that the Calliphoridae are distinct from the Muscidae and that their closest affinities within the Muscoidea are with the Anthomyiidae from which both they and the Muscidae arose. On the basis of both larval and genitalic characters, the Calliphoridae are also closer to the Anthomyiidae than the other family of the Sarcophagoidea, the Sarcophagidae. Most calliphorids show less divergence in such characters as the posterior depression and the posterior spiracles. This depression is absent in the Anthomyiidae, figs. 39, 43, and 47, absent to moderate in the Calliphoridae, figs. 41, 45, and 49, and is well developed in the Sarcophagidae, figs. 42, 46, and 50. The arrangement of the slits in the posterior spiracles of some Calliphoridae, figs. 56, 76, and 83, is like that of the Anthomyiidae, as in figs. 51 and 52. The arrangement in the Sarcophagidae, as in figs. 70 and 85, is much farther removed from the anthomyiid type. Also the male genitalia of the Calliphoridae are much closer to those of the Anthomyiidae than are those of the Sarcophagidae.

The Sarcophagidae are here divided into two subfamilies, the Miltogramminae and the Sarcophaginae on the bareness or plumosity of the antennal arista respectively. Hall (1932) has proposed a new subfamily to accommodate the genus *Sarothromyia*, on the basis of the presence of a button in the larval posterior spiracle, fig. 57, and the lack of the posterior cavity, fig. 101. The adult differs from the other Sarcophaginae in the shape of the head. Since the adult is similar in most respects to the Sarcophaginae and the button of the larva, though in vestigial form, is present in other sarcophagine larvae, it

---

EXPLANATION OF PLATE II

Third instar larvae, buccal armatures: FIG. 20. *Mesembrina meridiana* Linn. (after Thomson 1937). FIG. 21. *Haematobia stimulans* Meig. (after Thomson 1937). FIG. 22. *Stomoxys calcitrans* Linn. FIG. 23. *Stomorhina lunata* Fabr. (after Hall 1948). FIG. 24. *Calliphora vicina* Rob.-Desv. (after Hall 1948). FIG. 25. *Phormia regina* Meig. (after Hall 1948). FIG. 26. *Callitroga americana* Cushing & Patton (after Hall 1948). FIG. 27. *Pollenia rudis* Fabr. (after Hall 1948). Second instar, same: FIG. 28. *Senotainia trilineata* Van der Wulp (after Allen 1926). Third instar, same: FIG. 29. *Brachycoma sarcophagina* Tns. FIG. 30. *Sarothromyia femoralis* var. *simplex* Aldrich (after Hall 1932). FIG. 31. *Wohlfahrtia vigil* Walk. (after Walker 1937). FIG. 32. *Sarcophaga stimulans* Van der Wulp. FIG. 33. *Sarcophaga bullata* Park. FIG. 34. *Oestrus ovis* Linn. FIG. 35. *Cuterebra buccata* F. (after Knipling and Brody 1940). FIG. 36. *Orthellia cornicina* F., dorsal view (after Thomson 1937).


20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
OH
HS
VCN
DCN

seems more expressive of kinship to regard *Sarothromyia* as simply an aberrant genus of Sarcophaginae. Larvae of the family Sarcophagidae outside of the genera *Sarcophaga* and *Wohlfahrtia*, are not plentiful and perhaps the rearing of more genera close to *Sarothromyia* will give more evidence to support the Sarothromyiinae.

The Miltogramminae have previously been allied with the Larvaevoridae on the basis of the bare arista. However the nature of the buccal armature, figs. 28, 29, and the lack of a mesothoracic postnotum in the adults deny this relationship. Their general characteristics are essentially sarcophagoid.

The dorsal cornual cleft of the Sarcophagidae, figs. 28 to 33, has in all probability developed from the dorsal window of the Anthomyiidae, figs. 1 to 6. *Stomorhina lunata* Fab., a calliphorid, may have been an intermediate form. Its pharyngeal sclerite, fig. 23, is more suggestive of that of the Sarcophagidae than it is of most calliphorid pharyngeal sclerites. As can be seen in fig. 23, the dorsal cornua is high and is slightly cleft in a manner similar to that found in the Sarcophagidae.

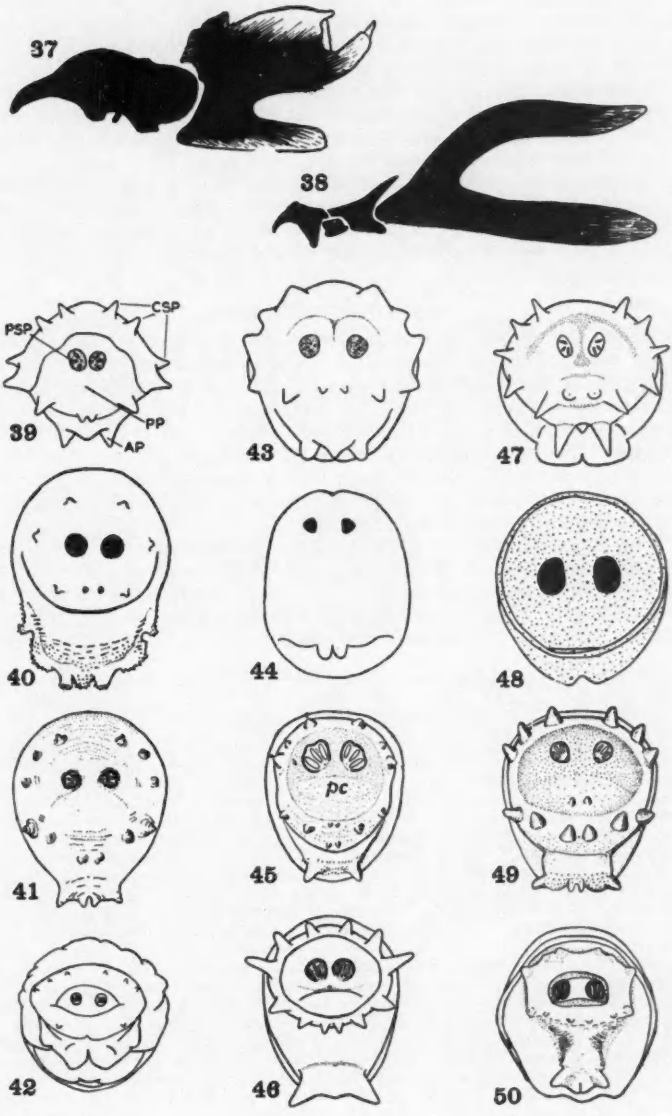
Whether the Sarcophagidae developed independently from ancestral anthomyiid stock or through a calliphorid such as *Stomorhina lunata* Fab. is still an open question. The evidence, however, seems to point to a development of the Sarcophagidae from primitive calliphorid-like stock.

The superfamily Oestroidea is tentatively divided into the Larvaevoridae and the Oestridae. Insufficient larval material was available in the Larvaevoridae to treat the family in any detail. On the basis of the buccal armature, fig. 35, the genera formerly placed in the Cuterebridae are here included in the Oestridae. It is hoped that in the future it will be possible to treat this entire superfamily in more detail.

The Oestroidea show certain affinities to the Sarcophagoidea in the genitalia. The larvae of the Oestroidea, however, are entirely parasitic and the nature of their buccal armature, figs. 34, 35, and posterior spiracles is often quite different from the corresponding structures in the Sarcophagoidea, figs. 23 to 33, and Muscoidea, figs. 1 to 22. The larvae indicate that the Oestroidea are farther removed from both the Sarcophagoidea and Muscoidea than the latter are from each other. In the adults the development of the mesothoracic postnotum, except in the Cuterebridae, and the nature of the second abdominal sternite, figs. 124–126, further serve to differentiate them.

EXPLANATION OF PLATE III

Third instar larvae, buccal armature: FIG. 37. *Phryxe vulgaris* Fall. (after Bisset 1938). FIG. 38. *Phyto melanocephala* Meig. (after Thomson 1934). Third instar larvae, posterior plates: FIG. 39. *Scopeuma* sp. FIG. 40. *Synthesiomyia nudiseta* Van der Wulp (after Siddons and Roy 1942). FIG. 41. *Calliphora vicina* Rob.-Desv. (after Hall 1948). FIG. 42. *Brachycoma sarcophagina* Tns. FIG. 43. *Fucellia* sp. FIG. 44. *Stomoxys calcitrans* Linn. FIG. 45. *Callitroga americana* Cushing and Patton (after Hall 1948). FIG. 46. *Sarcophaga ventricosa* Van der Wulp. FIG. 47. *Paregle cinerella* Fall. FIG. 48. *Morellia simplex* Loew (after Thomson 1937). FIG. 49. *Phaenicia caeruleiviridis* Macq. (after Hall 1948). FIG. 50. *Wohlfahrtia vigil* Walk. (after Walker 1937).


37
38
39
PSP
CSP
PP
AP
43
47
40
44
48
41
pc
45
49
42
46
50

The parasitism of the Oestroidea and particularly its limitation to certain groups of animals, Hexapoda for the Larvaevoridae and mammals for the Oestridae, indicates a high degree of specialization. This combined with their divergences (though some of these may be adaptive) from the anthomyoid stock could indicate a very early departure from the anthomyiid line or a parallel descent from the acalpytrate ancestors of the Anthomyiidae. The probable relationships of all the groups discussed here is shown in text fig. 1.

In general it can be said that the larvae offer as good if not better characters than the adults for indicating the relationships within the calyptrate muscoids. It is hoped that more of these larvae will be reared so that we may come to a better understanding of this large and complex group.

ECOLOGICAL RADIATION

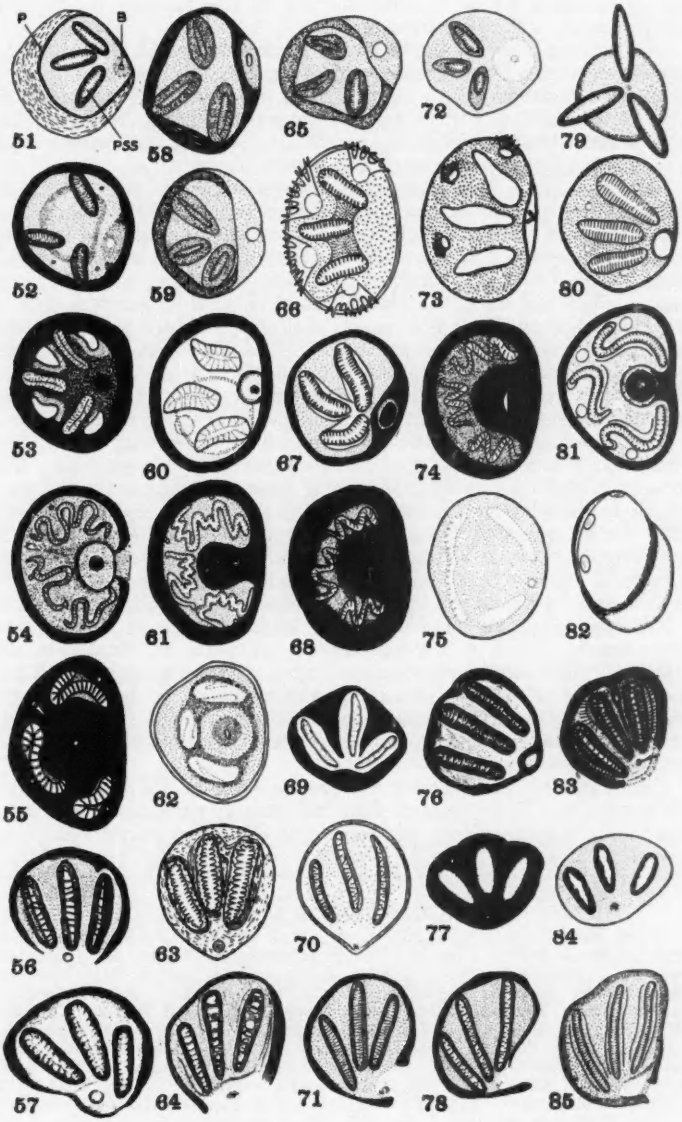
One of the interesting and important considerations in the evolution of the muscoid calyptrate Diptera is the development of their larval food habits. In regard to larval nutrition this group has undergone radial evolution. The larvae have branched out and occupied a great number of what we might call "nutritive zones." All the zones already occupied in various degree by larvae of the lower Diptera have been successfully invaded, in many cases with greater success than the older inhabitants. In addition, many new zones never before occupied by Diptera larvae have also been entered.

The lowest "nutritive zones" as far as the Diptera are concerned are the saprophagous, predaceous, and phytophagous zones in that order. Seventy-seven percent of dipterous families occupy one or more of these zones. The remaining twenty-three percent occupy the insect parasite, animal parasite, and coprophagous zones. The saprophagous

---

EXPLANATION OF PLATE IV

Third instar larvae, left posterior spiracular plates: FIG. 51. *Scopeuma* sp. FIG. 52. *Pucellia* sp. FIG. 53. *Limnophora exurda* Pand. (after Tate 1939). FIG. 54. *Morellia simplex* Loew (after Thomson 1937). FIG. 55. *Stomoxys calcitrans* Linn. (after Thomson 1937). FIG. 56. *Phormia regina* Meig. (after Hall 1948). FIG. 57. *Sarothromyia femoralis* var. *simplex* Ald. (after Hall 1932). FIG. 58. *Hylemya setiventris* Stein. FIG. 59. *Paregle cinerella* Fall. FIG. 60. *Mydaea pagana* Fabr. (after Thomson 1937). FIG. 61. *Mesembrina meridiana* Linn. (after Thomson 1937). FIG. 62. *Haematobia stimulans* Meig. (after Thomson 1937). FIG. 63. *Pollenia rudis* Fabr. (after Hall 1948). FIG. 64. *Wohlfahrtia vigil* Walk. (after Walker 1937). FIG. 65. *Hylemya antiqua* Meig. FIG. 66. *Hebecnema umbratica* Meig. (after Thomson 1937). FIG. 67. *Muscina pascuorum* Linn. (after Thomson 1937). FIG. 68. *Dasyphora cyanella* Meig. (after Thomson 1937). FIG. 69. *Stomorhina lunata* Fabr. (after Thomson 1937). FIG. 70. *Brachycoma sarcophagina* Tns. FIG. 71. *Sarcophaga ventricosa* Van der Wulp. FIG. 72. *Pegomya hyoscyami* Panz. FIG. 73. *Phaonia variegata* Meig. (after Thomson 1937). FIG. 74. *Orthellia cornicina* F. (after Thomson 1937). FIG. 75. *Atherigona* sp. FIG. 76. *Calliphora vicina* Rob.-Desv. (after Hall 1948). FIG. 77. *Senotainia vigilans* Allen, pupal spiracle, (after Allen 1926). FIG. 78. *Sarcophaga stimulans* Walk. FIG. 79. *Pegomya vanduzeei* Mall. FIG. 80. *Myiospila meditabunda* F. (after Thomson 1937). FIG. 81. *Polietes hirticrura* Meade (after Thomson 1937). FIG. 82. *Lispe sociabilis* Loew. FIG. 83. *Callitroga americana* Cushing and Patton (after Hall 1948). FIG. 84. *Phrosinella fulvicornis* Coq., pupal spiracle, (after Allen 1926). FIG. 85. *Sarcophaga bullata* Park.


P
B
PSS
51
58
65
72
79
52
59
66
73
80
53
60
67
74
81
54
61
68
75
82
55
62
69
76
83
56
63
70
77
84
57
64
71
78
85

zone is occupied by forty-eight percent of the families of Diptera, including most of the Nematocera.

It is probable that the anthomyiid stock from which the remainder of the calyptrate muscoids arose, and its turn was derived from otitid or helomyzid ancestors. Both these families are essentially saprophagous in the larval stage, and this feeding habit is found in the Anthomyiidae, particularly in the more primitive forms. Above this, the Anthomyiidae have invaded the phytophagous and coprophagous zones.

The Fanniidae and Muscidae are very closely related to the Anthomyiidae on morphological characteristics and this relationship is also evident in the food habits. Except for the Muscidae striking out into the predaceous zone there has been no radical advance in food habits. The Fanniidae have entered the saprophagous and coprophagous zones and many of its members can feed on either type of food. The Muscidae, in which the hooks, though appressed, are capable of independent movement, are predaceous. As the hooks became fused, asymmetrical and more spatula-like, an offshoot of the main stem invaded the coprophagous zone. Many of these same forms have also been able to enter the saprophagous zone. This is shown in text figure 2.

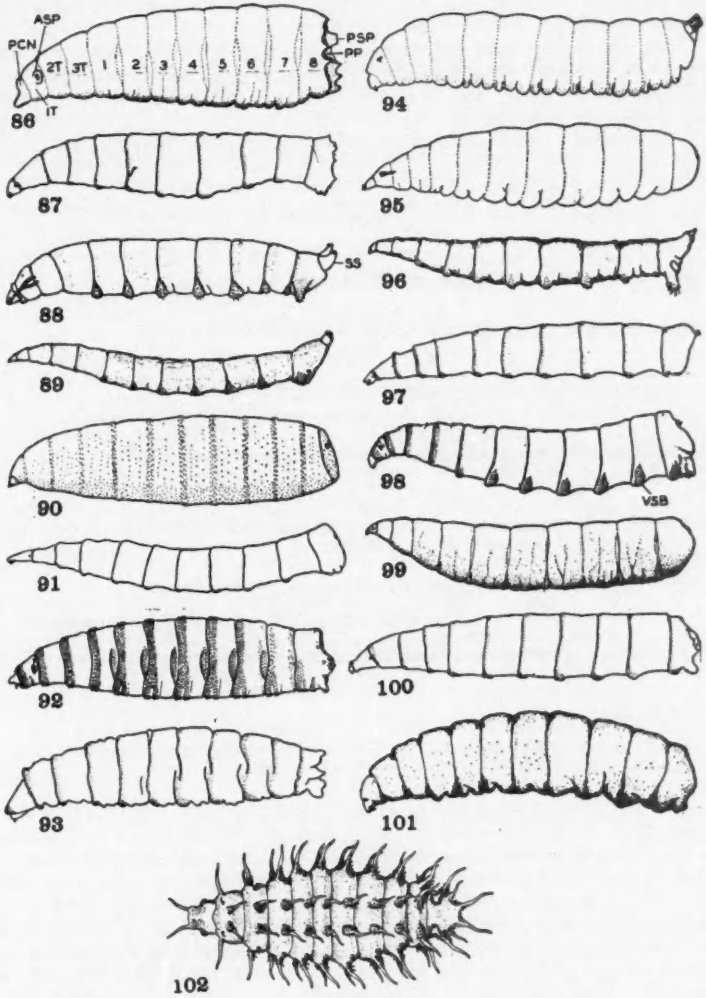
The two families of the Sarcophagoidea are so similar in nutritive habits that it is simpler to consider the superfamily as one unit. The Sarcophagoidea have advanced greatly over the Muscoidea in larval nutrition. Besides having entered the coprophagous and insect parasitism zones, they have successfully invaded three new zones, the sarcophagous, facultative parasitism of animals and obligate parasitism of animals. In the Sarcophagoidea we have some of the first forms to enter living mammalism tissue. Obligate mammalian parasitism is obviously a recent incursion, only seven species being definitely incriminated. Quite a few species are parasitic in Amphibia and Mollusca. The occasional parasitic forms are very numerous. These flies normally oviposit in decaying animal tissue or dung, but will oviposit in sores and wounds and develop there. Probably they represent a transitional stage between sarcophages and obligate animal parasites.

Parasitism by the Diptera reaches its peak in the Oestridae and Larvaevoridae. Both these families are entirely parasitic in the larval stage. The Larvaevoridae have invaded the insect parasite zone, all

---

EXPLANATION OF PLATE V

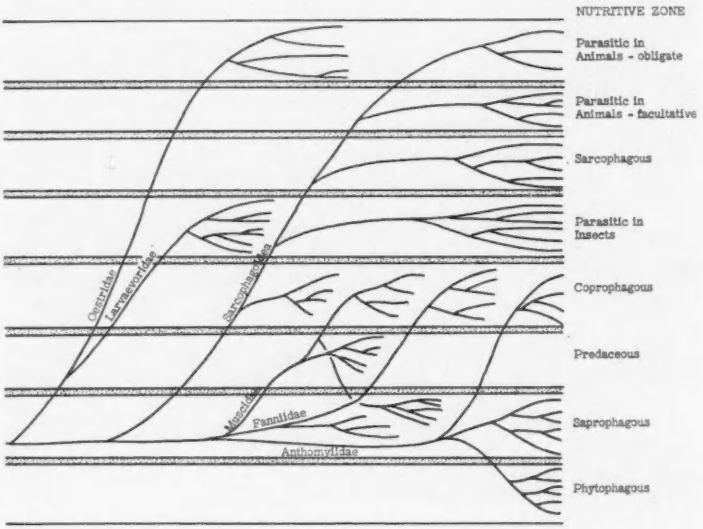
Third instar larvae, lateral views of bodies: FIG. 86. *Hylemya variata* Fall. (after Thomson 1937). FIG. 87. *Paregle cinerella* Fall. FIG. 88. *Limnophora exurda* Pand. (after Tate 1939). FIG. 89. *Limnophora torryae* Joh. (after Johannsen 1935). FIG. 90. *Morellia simplex* Loew (after Thomson 1937). FIG. 91. *Stomoxys calcitrans* Linn. FIG. 92. *Callitroga americana* Cushing and Patton (after Hall 1948). FIG. 93. *Sarcophaga bullata* Parker. FIG. 94. *Mydaea pagana* Fabr. (after Thomson 1937). FIG. 95. *Hebecnema umbratica* Meig. (after Thomson 1937). FIG. 96. *Limnophora* (*Lispoides*) *aequifrons* Stein (after Johannsen 1935). FIG. 97. *Lispe sociabilis* Loew. FIG. 98. *Synthesiomyia nudiseta* Van der Wulp (after Siddons and Roy 1942). FIG. 99. *Polietes hirticrura* Meade (after Thomson 1937). FIG. 100. *Calliphora vomitoria* Linn. FIG. 101. *Sarothromyia femoralis* var. *simplex* Aldrich (after Hall 1932). FIG. 102. *Fannia canicularis* Linn., dorsal view, (after Hewitt 1912).


ASP
PCN
PSP
PP
2T
3T
1
2
3
4
5
6
7
8
9
IT
SS
VSB
86
87
88
89
90
91
92
93
94
95
96
97
98
99
100
101
102

being obligate parasites in insects. This zone has been invaded before, but only by small families, such as the Conopidae and Pyrgotidae. The Larvaevoridae have been more successful than any other Diptera in this zone. Its only abundant competitors in this zone are the parasitic Hymenoptera.

The Oestridae have successfully gone into obligate parasitism in mammals. Their parasitism is of a very high type. Unlike the Larvaevoridae, which kill the host, the oestrids leave the host alive for succeeding generations.

The above relationships are shown graphically in text figure 2.



TEXT FIG. 2. The ecological radiation of the calyptrate muscoid Diptera.

In the light of what has been presented, the logical question is why have the calyptrate muscoids been able to invade these new zones, not previously invaded by the Diptera. There must have been some fundamental change in the digestive system in order for them to be able to enter these new zones. There does not seem to be enough morphological difference between the larvae of an anthomyiid and a sarcophagid to account for their ability to feed on such different food materials as cellulose and protein. The fundamental change must have been in the digestive enzymes, perhaps with some accompanying changes in general physiology. Along with these enzyme differences we must assume accompanying differences in the genes or gene chains controlling the production of these enzymes. It seems logical to assume that these larvae were somehow preadapted for these zones and that when acci-

dentally placed in a situation where selection pressure favored the ability to digest these new foods, they were able to survive and develop to maturity. The accidental deposition of sarcophagid larvae in wounds is a good example of this. This may also be an explanation of why the calyptrate muscoids have been able to radiate into so many "nutritive zones."

The evidence on the evolution of larval food habits in the Diptera is by no means complete. The number of forms whose food habits are unknown is numerous, in fact there are probably more unknown than known. Also our knowledge of their digestive enzymes is far from complete. A comparative study of the digestive enzyme systems of extant forms would do much to clear up the physical as well as the nutritional evolution of the calyptrate muscoids and the other families of Diptera.

DIAGNOSIS AND CHARACTERISTICS

KEY TO FAMILIES

Adults

1. Either mesothoracic postnotum strongly biconvex or mouthparts reduced, often vestigial; edges of abdominal sternites usually overlapped and partially hidden by margins of tergites, fig. 124; apical cross vein present 2
   Mesothoracic postnotum not strongly developed; mouthparts not reduced; first abdominal sternite usually overlaps lateral margins of tergites, figs. 125, 126 3
2. Mouthparts reduced or vestigial; body may be pilose, never bristled; hypopleura with long hairs; parasitic in mammals ..... **Oestridae**
   Mouthparts seldom reduced or vestigial; body generally well bristled; hypopleura with row of bristles, never pilose; endoparasites in insects, ... **Larvaevoridae**
3. Hypopleura with weak hair or bare; pteropleuron lightly pilose or bare 4
   Hypopleura with one or more rows of bristles below metathoracic spiracle; pteropleura setose 6
4. Sixth vein reaches hind margin of wing, at least as fold, figs. 103, 110; one sternopleural bristle present or undersurface of scutellum with fine erect hairs, fig. 119 (except *Fucellia* and a few Scopeumatinae); arista never pectinate only above ..... **Anthomyiidae**
   Sixth vein never reaches hind wing margin, figs. 105 to 109 and 111 to 116; normally more than one sternopleural bristle; undersurface of scutellum generally without fine erect hairs; arista may be pectinate only above, fig. 120 5
5. Seventh vein curves around toward sixth so that if extended they would meet before wing margin, fig. 104; only two sternopleurals present, ... **Fanniidae**
   Seventh vein not as above; sixth and seventh veins if extended would not meet before wing margin, figs. 105 to 107, 111 to 113, and 115; usually two to four sternopleurals ..... **Muscidae**
6. Intrapostocular cilia present; two notopleural bristles; propleuron and prosternum pilose (except Polleniinae); arista with plumosity extending to apex; body with metallic blue, green, bronze or black ..... **Calliphoridae**
   Intrapostocular cilia absent 7
7. Arista plumose, pubescent or bare; if plumose, plumosity never extends to apex; propleuron and prosternum usually bare; pile, if present, never large or thickly set; two to four notopleural bristles; abdomen usually grey or black tesselated ..... **Sarcophagidae**
   Arista pectinate or propleuron and prosternum pilose; abdomen olivaceous to bluish green or body medium sized, glabrous black ..... **Calliphoridae**

Larvae (Third Instar)

1. Pharyngeal sclerite large, with heavily pigmented base, cornua non-pigmented, figs. 34, 35; posterior spiracular plates ovoid or reniform with many closely packed openings; parasitic in mammals.....**Oestridae**
   Pharyngeal sclerite not as above; posterior spiracular plates not with many closely packed openings..... 2
2. Pharyngeal sclerite generally robust and well pigmented; cornua diverging widely, fig. 38, or highly modified and reduced, fig. 37; parastomal bars and windows never present; posterior spiracular plates may bear several sinuate slits or three ovoid slits; endoparasites in insects.....**Larvaevoridae**
   Pharyngeal sclerite moderately pigmented and robust as in figs. 1 to 33; parastomal bars and windows may be present; posterior spiracles never with more than three slits, figs. 51 to 85; mostly saprophagous or phytophagous, a few carnivorous or parasitic..... 3
3. Posterior spiracular slits sinuate, long or short, figs. 54, 61, 68, 74, 81, and 55, 62.....**Muscidae** (pt.)
   Posterior spiracular slits linear, long ovoid or circular, as in figs. 51 to 53, 58 to 60, 65 to 67, 72, 83, and 75 to 78..... 4
4. Lowest spiracular slit slants lateroventrally from button, figs. 51 to 53, 58 to 60, 65 to 67, 72, 73, 75, and 80; or openings circular, fig. 82; posterior spiracular plates never in depression, may be raised on short stalks, figs. 79, 88; oral hooks fused or separate..... 5
   Lowest (or outer) spiracular slit never slants below horizontal, figs. 56, 57, 63, 64, 69 to 71, 76 to 78, and 83 to 85; always linear; posterior spiracular plates generally in depression, figs. 41, 42, 45, 46, 49 and 50; never raised on stalks; parastomal bars present and oral hooks separate..... 7
5. Larva depressed; with four rows of spiniferous tubercles along its length, fig. 102; cornua without windows and not flaring, fig. 7; oral hooks separate.....**Fanniidae**
   Larvae cylindrical and tapering, figs. 86 to 101; no spiniferous tubercles; cornua may have windows and vertical flaring; oral hooks separate or fused..... 6
6. Oral hooks closely appressed or fused, fig. 36; cornua not flaring and without windows, figs. 8 to 22; posterior plate generally without papillae, figs. 44, 48.....**Muscidae**
   Oral hooks separate; cornua with flaring and windows, fig. 1 and 3 to 6; posterior plate generally with papillae, figs. 39, 43 and 47; if not, spiracles are as in fig. 79.....**Anthomyiidae**
7. Dorsal cornua deeply incised, figs. 28 to 33; posterior spiracular plates generally in deep cavity (except *Sarothromyia*), figs. 42, 46 and 50; posterior spiracles as in figs. 57, 64, 70, 71, 77, 78, 84, and 85.....**Sarcophagidae**
   Dorsal cornua not deeply incised, figs. 23 to 27; posterior spiracular plates at most in shallow cavity, figs. 41, 45, and 49; posterior spiracles as in figs. 56, 63, 69, 76, and 83.....**Calliphoridae**

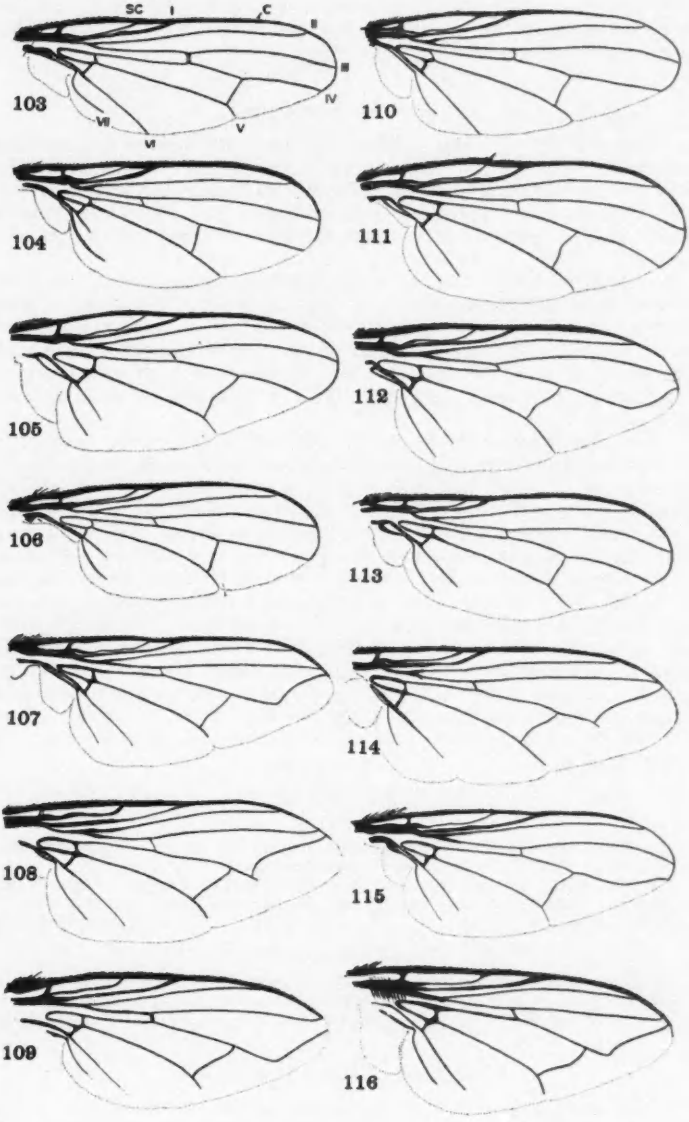
Superfamily **Muscoidea**

The adults of this family are small grey pollinose or black iridescent flies. In North America this superfamily is composed of three families, the Anthomyiidae, Fanniidae, and Muscidae. Larvae of the Muscidae

---

EXPLANATION OF PLATE VI

Adults, wings: FIG. 103. *Scopeuma stercoraria* Linn. FIG. 104. *Euryomma communis* Walk. FIG. 105. *Limnophora* (*Lispoides*) *aequifrons* Stein. FIG. 106. *Lispe albitarsis* Stein. FIG. 107. *Musca domestica* Linn. FIG. 108. *Sarcophaga bullata* Park. FIG. 109. *Huascaromusca formosa* Aldrich (after Hall 1948). FIG. 110. *Hylemya cilicura* Rond. FIG. 111. *Phaonia fusca* Stein. FIG. 112. *Muscina pascuorum* Linn. FIG. 113. *Macrorchis ausoba* Walk. FIG. 114. *Senotainia trilineata argentifrons* Tns. FIG. 115. *Stomoxys calcitrans* Linn. FIG. 116. *Phormia regina* Meig. (after Hall 1948).


SC
I
C
II
III
IV
V
VI
VII
103
104
105
106
107
108
109
110
111
112
113
114
115
116

have their oral hooks closely appressed or apparently fused. In the other two families the oral hooks are well separated. Many of the larvae of this superfamily are predaceous.

Family **Anthomyiidae**

Adults—Body not large; glabrous to grey-pollinose in texture and lmoderately spinose; proboscis generally not longer than head height abella not greatly expanded; palpi filiform to slightly expanded; arista; bare, pubescent, or plumose; both reclinate and proclinate fronto-orbitals usually present; two to four frontals; cruciate frontals present or absent.

Stenopleuron with one to four bristles; normally two humeral bristles; generally some presutural acrosticals; two presutural dorso-centrals; scutellum typically with one pair of lateroscutellars, one pair of discoscutellars and one pair of apicoscutellars; erect hairs may be present on undersurface, fig. 119. Wings with sixth vein reaching wing margin, at least as a fold, figs. 103, 110; calypteres small and about equal in size.

Third instar larva—Body slender, fig. 87, and tapering anteriorly or more stubby in form, fig. 86; always circular in cross section; body surface bare or with last few segments covered with black spines; posterior plate with twelve to fourteen circumspiracular papillae, figs. 39, 43, and 47; if papillae indistinct (*Pegomya vanduzeei* Mall.), posterior spiracular openings mounted on small tubercle and without peritreme, fig. 79; buccal armature as in figs. 1 to 6; oral hooks separate; may be sharp, blunt, or toothed; no accessory sclerites around hooks; parastomal bars often present; dorsal and ventral cornua flare in vertical plane; each generally with small subterminal window; ventral pharyngeal ridges usually present; posterior spiracular plates never in depression; peritreme always closed and button distinct; slits elongate oval and radiating from button, figs. 51, 52, 58, 59, 65, 72, and 79; never narrow as in fig. 71, or sub-parallel; lowest or outer slit runs latero-ventrally from button.

KEY TO SUBFAMILIES

Adults

1. Scutellum with fine erect hairs on undersurface, fig. 119 ..... **Anthomyiinae**
   Scutellum without fine erect hairs on undersurface 2
2. Cruciate frontals present, generally four sternopleurals. *Fucellia* .. **Anthomyiinae**
   Cruciate frontals absent; generally one sternopleural, two or three present in a few species ..... **Scopeumatinae**

Third Instar Larvae

1. Body generally free from spines except at intersegmental ridges .. **Anthomyiinae**
   Body with last few segments almost entirely covered with short, sharp spines (only *Scopeuma* sp. studied) ..... **Scopeumatinae**

Subfamily **Scopeumatinae**

There are approximately 33 genera of this subfamily in North America; adults have been studied of representatives of eleven of these and the larva of only the genus *Scopeuma*.

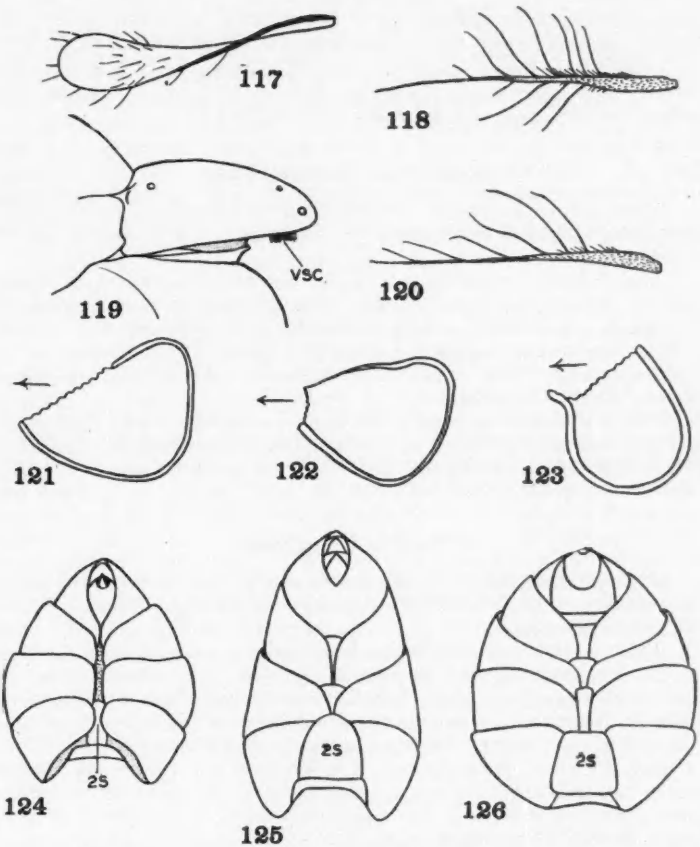


FIG. 117. *Lispe nasoni* Stein, left maxillary palpus, ventral view. FIG. 118. *Lispe nasoni* Stein, arista. FIG. 119. *Anthomyia pluvialis* Linn., lateral view of scutellum. FIG. 120. *Stomoxys calcitrans* Linn., arista. FIG. 121. *Musca domestica* Linn., left lower calypter. FIG. 122. *Muscina pascuorum* Linn., left lower calypter. FIG. 123. *Phaonia fusca* Stein, left lower calypter. FIG. 124. Larvaevoridae, ventral view of abdomen. FIG. 125. Sarcophagidae: Miltogramminae, ventral view of abdomen. FIG. 126. Sarcophagidae: Sarcophaginae, ventral view of abdomen.

Adult.—Boby glabrous to grey pollinose; sometimes extremely pilose; frons equal in both sexes; cruciate frontals generally not present; oral vibrissae variable; presutural acrosticals poorly defined; two or three sternopleurals present in a few genera; abdomen base often narrow; abdomen may appear petiolate; usually six visible tergites.

Third instar larva.—Body round and tapering; last few segments covered with short sharp spines in addition to those at the intersegmental borders; posterior spiracles as in figure 51.

Subfamily **Anthomyiinae**

There are 23 genera of this subfamily in North America; adults have been studied of representatives of nineteen of these and the larvae of four.

Adult.—Body normally grey pollinose; frons narrowed in males; cruciate frontals generally present; oral vibrissae present; presutural acrosticals often distinct, three in number; sternopleurals 1–1, 2–1, or 2–2; abdomen never appearing petiolate; five visible tergites.

Third instar larva.—Larvae of four genera have been studied or drawn from the literature.

Body round and tapering, figs. 86 and 87; no spines except at intersegmental ridges; posterior spiracles either three ovoid slits radiating from button, figs. 52, 58, 59, 65, and 72, or three slits mounted on a tubercle and without peritreme, fig. 79.

Family **Fanniidae**

There are four genera of this family in North America; adults have been studied of representatives of three of these and the larva of only the genus *Fannia*.

Adult.—Body small and greyish pollinose in color; often with light spots on abdominal tergites; proboscis short with fleshy labellum; palpi not expanded; arista bare or lightly pubescent; three to six frontals; frontoorbitals present; anterior frontoorbital often divaricate; cruciate frontals absent; inner and outer verticals present.

Generally two sternopleurals, a weak third one sometimes present; one or two presutural dorsocentrals; scutellum with two lateroscutellars, two discoscutellars and two apicoscutellars; calypteres relatively small, lower slightly larger than upper.

Third instar larva.—Body depressed and surface roughened, fig. 102; first and last segments obliquely truncate; second and third thoracic segments and first seven abdominal segments with dorsal, laterodorsal, and lateroventral pairs of projections; eighth abdominal segment with six tubercles around border; short spines and tubercles ventrally on segments; buccal armature as in figure 7; oral hooks separate, narrow and curved; no accessory sclerites around hooks; pharyngeal sclerite not flaring vertically and without windows; posterior spiracles on relatively long tubercles; consist of three lobes with a spiracular opening at extremity of each lobe.

Family **Muscidae**

Adult.—Small to medium flies; body normally grey pollinose, sometimes metallic blue or green in color; proboscis may be longer than head; labellum large and fleshy; proboscis rigid and with reduced labellum in Stomoxyinae; palpi filiform to spatulate; arista bare, pubescent, or plumose; two to nine frontals, no to four frontoorbitals; one or two pair of verticals; cruciate frontals may be present.

Sternopleuron generally with two to four bristles; only one in *Stomoxys calcitrans* Linn.; two or three humeral bristles; acrosticals usually indistinct; two presutural dorsocentrals; scutellum generally with more than one pair of lateroscutellars; hairs on undersurface of scutellum present in a few Phaoniinae.

Wings as in figs. 105 and 107, 111 to 113, and 115; fourth vein may be sharply curved forward; calypteres large; lower distinctly larger than upper.

Third instar larva.—Body as in figs. 88 to 91 and 94 to 99, generally slender and tapering anteriorly; not spinose; first thoracic segment infrequently ringed with spines; posterior plate, figs. 40, 44, and 48, generally smooth and rounded; never any large circumspiracular papillae; a few small ones present in *Synthesiomyia nudista* Van der Wulp, fig. 40; larvae of *Limnophora* and *Lispoides* with either larvapods or an extremely heavy spine band ventrally on eighth abdominal segment; buccal armature as in figs. 8 to 22; oral hooks fused or so closely appressed as to appear fused, fig. 36; hooks often unequal in length, figs. 21 and 22, and with complex arrangement of accessory sclerites, figs 8 to 15; dental sclerites may form ventral bridge; cornua of pharyngeal sclerite unequal in size and without windows, seldom exhibiting any flaring in the vertical plane; pharyngeal ridges present or absent; posterior spiracular plates, figs. 53 to 55, 60 to 62, 73 to 75, 80 to 82, either flush with posterior plate, fig. 90, or on stalks of varying length, fig. 96; peritreme, if present, entire; slits variable in shape and arrangement; there may be three long ovoid slits radiating from button, figs. 53, 60, and 67, three narrow slits in circle which includes button, fig. 75, three small ovoid openings along edge of wedge-shaped stalk, fig. 82, or three short sinuate slits in an arc which may include the button, figs. 54, 61, 68, 74 and 81.

KEY TO SUBFAMILIES

Adults

1. Mouthparts elongate and rigid; arista pectinate only above, fig. 120, one or two sternopleurals ..... **Stomoxyinae**
   Mouthparts short and not rigid; arista variable, never pectinate only above, two to four sternopleurals 2
2. Palpi flattened and expanded distally, fig. 117, parafacialia almost always setulose; frons equal in both sexes; arista as in fig. 118 ..... **Lispinae**
   Palpi not as above; frons may or may not be equal in both sexes; arista not as in fig. 118 3
3. Lower calypter triangular, figs. 121, 122; truncate at apex with inner margin close to scutellum; three humeral bristles; fourth vein generally ending before wing tip, figs. 107 and 112; males with frons narrow 4
   Lower calypter rounded at apex, fig. 123; inner margin diverging from scutellum; normally two strong or two strong and one weak humeral bristles; fourth vein normally ends behind wing tip, figs. 105, 106, 111, 113, and 115; frons variable 5

4. Three strong lateroscutellars; scutellum flattened dorsally; arista plumose; wing as in figure 112; lower calypter as in figure 122; large bluish species. *Muscina pascuorum* Linn. . . . . **Phaoniinae**
Normally two lateroscutellars; if three, arista is not plumose; scutellum not flattened dorsally; lower calypter as in figure 121. . . . . **Muscinae**
5. One strong reclinate frontoorbital present; one strong or one strong and one weak presutural dorsocentral; sternopleurals, if three, in an equilateral triangle; frons equal in both sexes. . . . . **Coenosiinae**
At least two frontoorbitals present; one of these may be proclinate; normally two equal presutural dorsocentrals; sternopleurals, if three, never in equilateral triangle; frons variable. . . . . **Phaoniinae**

Third Instar Larvae

1. Posterior spiracles borne on short stalks or sclerotized projections, figs. 88, 89, 94, 96 and 97. 2
Posterior spiracles either flush with the posterior plate or only slightly raised, figs. 90, 91, 95, 98, and 99. 5
2. Posterior spiracles at tip of moderately long stalks, figs. 88, 89, 96, their bases close together; spiracular slits when distinct as in figure 53; buccal armature as in figures 12, 13; larvapods may be present at eighth abdominal segment, figs. 88, 89, and 96; aquatic, some *Limnophora*. . . . . (**Phaoniinae**)
Posterior spiracles on short sclerotized stalks, separate at base, figs. 94 and 97. 3
3. Spiracular slits, three elongate ovals radiating from button, figs. 53, 60, 66, 67, 73, 80. . . . . **Phaoniinae**
Spiracular slits, either three slits in circle including button, fig. 75, or three small ovals in arc, fig. 82; never radiating from button. 4
4. Spiracular slits, three short ovals in arc along outer margin of spiracular plate, fig. 82; plates facing slightly mesad; pharyngeal sclerite with long narrow pharyngeal groove, fig. 15; based on *Lispe sociabilis* Loew. . . **Lispinae**
Spiracular slits three long ovals forming ring which includes the button, fig. 75; spiracular plate not tilted as above; pharyngeal groove short and wider, fig. 14; based on *Atherigona* sp. . . . . **Coenosiinae**
5. Spiracular slits three long ovals radiating from button, figs. 53, 60, 66, 67, 73, 80; some genera of. . . . . **Phaoniinae**
Spiracular slits sinuate, in arc or circle; never radiating fanwise from button. 6
6. Spiracular slits highly sinuate, often long; arranged in arc of circle to one side of button or including button, figs. 54, 61, 68, 74, and 81. . . . . **Muscinae**
Spiracular slits very slightly sinuate, short, arranged in circle around the button, figs. 55, 62. . . . . **Stomoxyinae**

Subfamily **Coenosiinae**

There are ten genera of this subfamily in North America; adults have been studied of representatives of eight of these and the larva of *Atherigona* sp.

Adult.—Small greyish or yellowish-grey pollinose flies; frons equal in both sexes; proboscis short, palpi not expanded; arista pubescent or lightly plumose; two or three frontals and one or two pairs of verticals present.

Thorax with two humerals; sternopleurals normally three, if four (*Bithoracochaeta*), in 2–2 arrangement; discoscutellars weak if present; wings as in fig. 113.

Third instar larva.—Body elongate, slender, devoid of spines; buccal armature as in fig. 14; cornua slightly flaring.

Subfamily **Lispinae**

There is one genus of this subfamily in North America; adults have been studied of this genus (*Lispe*) and the larva of *Lispe sociabilis* Loew.

Adult.—Body moderately robust, greyish pollinose; frons equal in both sexes; proboscis short; arista, fig. 118, with ten to fourteen hairs above and only four below; usually four frontals, two reclinate fronto-orbitals and two pair of verticals present; cruciate frontals not present.

Thorax with two presutural dorsocentrals and three sternopleurals; scutellum with one pair of lateroscutellar and one pair of apicoscutellars; discoscutellars very weak, if present; wings as in fig. 106.

Subfamily **Phaoniinae**

There are forty genera of this subfamily in North America; adults have been studied of representatives of thirty-two of these and the larvae of seven.

Adult.—Body moderately robust; greyish pollinose or metallic; frons generally narrower in males than females; proboscis short, labellum expanded; palpi slightly expanded but never spatulate; arista bare, pubescent, or plumose; in females and dichoptic males, two to six frontals and inner and outer verticals present; only frontals and verticals present in holoptic males.

Thorax with two strong humerals, weak third sometimes present; two to four sternopleurals, never in equilateral triangle; scutellum generally with three pairs of lateroscutellars; two of these may be weak; small discoscutellars often present; erect hairs may be present on undersurface of scutellum; wing as in figs. 105, 111, and 112.

Third instar larva.—Body broad, figs. 94, 95, or elongate and narrow, figs. 88, 89; buccal armature as in figs. 8 to 13.

Subfamily **Muscinae**

There are nine genera of this subfamily in North America; adults of representatives of three of these have been studied and the larvae of six.

Adult.—Body moderately robust; grey pollinose to metallic blues and greens in color; frons narrower in males than in females; proboscis short, labellum fleshy and expanded; palpi not expanded distally; arista bare pubescent or plumose; in females, frontals six or more and often very fine; frontoorbitals indistinct, proclinate if present.

Thorax with at least two presutural dorsocentrals; sternopleurals never in equilateral triangle; discoscutellars sometimes present; wings as in fig. 107.

Third instar larva.—Body slender or robust, figs. 90, 98; buccal armature as in figs. 16 to 20.

Subfamily **Stomoxyinae**

There are two genera of this subfamily in North America; adults and larvae of both have been studied.

Adult.—Body grey pollinose; frons narrower in males than in females; in female, about eight frontals present and several small bristles on frons below ocelli; frontoorbital area with several small proclinate bristles; two pair of verticals present.

Dorsal thoracic bristles often indistinct; two humerals, two notopleurals and two postalars present; scutellum with many small bristles in addition to scutellars.

Third instar larva.—Body slender and tapering anteriorly, fig. 91; almost devoid of spines; spiracular plates flush with posterior plate; buccal armature as in figs. 21, 22.

Superfamily **Sarcophagoidea**

The flies of this superfamily are moderately large and grey pollinose or iridescent green or blue in color. They possess hypopleural bristles, but lack a developed mesothoracic postnotum. This superfamily has often been lumped into one group with the Oestroidea, but on the basis of larval characters is here considered as a separate unit.

Family **Calliphoridae**

This section is adapted from Hall (1948), which adequately defines the group and its subfamilies as accepted here. The descriptions have been reduced. Some information on larval material has been added from personal observation.

Adult.—Clypeus flush to deeply impressed, most often half as wide as long; cheek grooves deep; palpi filiform, cylindric or clavate, sometimes flat; arista very rarely pectinate, pubescent or bare; vertex narrower in male than in female; intrapostocular cilia present except in Rhiniinae and occasional specimens of *Onesia* and Melanodexiini.

Thorax without mesothoracic postnotum except in Mesembrinellinae; postnotum slightly raised here; pteropleuron usually setose on posterior half or slightly more; notopleuron setose; wings with fourth vein angularly, fig. 116, or roundly, fig. 109, bending toward apex; genital segments of male small to large.

Third instar larva.—Body cylindrical and tapering at both ends, figs. 92, 100; ventral spine bands and annuli found on most segments; lateral spined bands often found on abdominal segments; posterior spiracles in slight depression in posterior plate; buccal armature as in figs. 23 to 27; accessory sclerites absent except in Calliphorini, fig. 24; dorsal cornua appearing incised only in *Stomorhina*, fig. 23; often a variably pigmented area present above dorsal cornua; posterior spiracular plates as in figs. 56, 63, 69, 76, and 83; peritreme closed or open and button distinct or indistinct; slits run latero-dorsally from button; often subparallel.

KEYS TO SUBFAMILIES

Adults

1. Mesothoracic postnotum small, but distinct; metathoracic spiracle ovate and very large, the opening on the dorsal margin; fourth vein, fig. 109, with a broad sinuous curve toward costal margin; bucca narrow, hardly one-fifth eye height ..... **Mesembrinellinae**
   Mesothoracic postnotum not developed; metathoracic spiracle not as above; fourth vein, fig. 116, usually with a distinct angle; bucca distinctly higher in comparison with eye height 2
2. Remigium ciliate above 3
   Remigium bare above 4
3. Occipital orbits narrow; intrapostocular cilia inconspicuous or absent; greater ampulla bare or but faintly pubescent; lower calypter always bare on upper surface, rounded at apex, the lateral margin nearly straight ..... **Rhiniinae**

Occipital orbits wide; intrapostocular cilia distinct; greater ampulla often pilose or setose; lower calypter truncate posteriorly, concave on lateral margin, upper surface pilose at base to setose on disc (bare in *Hemilucilia* and *Chloroprocta*) ..... **Chrysomyinae**

4. Prosternum and propleuron setulose or pilose; vestiture of parafacials not reaching lower eye margin; thorax without crinkly hair ..... **Calliphorinae**
   Prosternum and propleuron bare; parafacials setose to lower eye margin; thorax with crinkly hair ..... **Polleniinae**

Third Instar Larvae

1. Larva with sclerotized area on ventral surface of third segment ..... **Mesembrinellinae**
   Larva without above sclerotized area 2
2. Spiracular peritreme open, button not enclosed, figs. 56, 83 ..... **Chrysomyinae**
   Spiracular peritreme closed, button enclosed, figs. 63, 69, 76 3
3. Button within closed peritreme which extends between each slit-like aperture, fig. 69 ..... **Rhiniinae**
   Peritreme not extending between slits 4
4. Peritreme well sclerotized and closed, fig. 76 ..... **Calliphorinae**
   Peritreme very weakly sclerotized; closed, fig. 63 ..... **Polleniinae**

Subfamily **Mesembrinellinae**

Adult.—Epistoma gently warped forward from clypeal plane, nearly as wide as clypeus; eye large, elongate oval, set nearly straight in head, bare; cruciate frontals present in female, absent in male; clypeus shrunken and shallow; parafacials bare; vibrissae slightly above oral margin; palpus clavate, thick apically; antennal base at or near middle of head in profile, bases approximate; arista with long ciliation above and below.

Thorax with propleuron bare; presupraalar bristle, one; prosternum narrowed posteriorly, widening anteriorly, setose; postalar bristles, two, one weak; post dorsocentral bristles three; scutellum with undersurface finely setose, the setae short; one discal and one apical bristle present; wings, fig. 109, without costal spine; remigium bare below; upper calypter small, bare, rounded; lower calypter, medium, ovate, bare.

Third instar larva.—Larvae developed within well defined uterus.

Subfamily **Rhiniinae**

Adult.—Occipital orbits narrow; epistoma generally protuberant.

Third instar larva.—Dorsal cornua having appearance of being divided, fig. 23.

Subfamily **Chrysomyinae**

Adult.—Frons narrower in males than in females; frontoorbitals absent in male; proclinate and reclinate frontoorbitals in female; facial carina absent or very slightly developed; antennal base at or slightly below middle of eye in profile; bases approximated or slightly separated; arista plumose above and below two-thirds to four-fifths the distance from base to apex.

Propleuron strongly pilose; propleural bristle strong; notopleural bristles normally two; scutellum generally without apical bristles; wings, fig. 116, without costal spine; remigium ciliate above posteriorly at base; male genitalia small and hidden.

Third instar larva.—Button absent or poorly defined and situated in gap in peritreme.

Subfamily **Calliphorinae**

Adult.—Epistoma warped forward from clypeal plane; bucca usually high in relation to eye height; vibrissae at or but slightly above oral margin and well separated; eye ovate and set more or less obliquely in head; outer verticals and proclinate frontoorbitals usually absent in males; arista with long cilia above and below, tip often bare.

Propleuron setose; prosternum setose; notopleural bristles two; intrapostsutural bristles absent; scutellum without apical bristles; remigium bare above and below; lower calypter large, posterior margin often wide.

Third instar larva.—Distinct button present.

Subfamily **Polleniinae**

Adults.—Bucca high, often one-half eye height or more; eye small, oblique; frons narrower in male than in female; frontal rows of bristles widely diverging in both sexes, converge in foremost one or two bristles; outer verticals absent in male; frontoorbitals absent in male; clypeus broad and shallow; vibrissae above oral margin; antennal bases distinctly separated by carina; arista plumose nearly to apex.

Thorax with three humeral bristles in straight line; sternopleurals two; prosternum large, wide, bulging anteriorly; spiracles small; scutellum with undersurface bare; with four strong lateral bristles; wings without strong costal spine; upper calypter small, rounded, bare; lower calypter large, long ovate, bare; genital segments of male, globose.

Third instar larva.—See key characters.

Family **Sarcophagidae**

Adult.—Frons narrower in males than in females; labellum generally expanded; palpi slightly clavate and setose; arista bare, pubescent, or plumose; if plumose, plumosity never extends to tip; clypeus variable from triangular and shallow to rectangular and deep; both verticals present; frontoorbitals two to four; frontals may extend down to the tip of the second antennal segment; parafacials often setulose.

Notum with two to four presutural and postsutural dorsocentrals; two to four notopleurals and two or three sternopleurals; apicoscutellars may be absent; propleuron and prosternum generally bare, sometimes with weak pile or bristles; fourth vein ends before wing tip, fig. 108; apical cell sometimes closed; abdomen with only marginal bristles.

Third instar larva.—Body as in figs. 93, 101; body surface often transversely wrinkled; spines generally present at intersegmental borders; some larvae without spines (*Brachycoma sarcophagina* Tns.); lateral pads usually present; posterior spiracular plates lie in a deep depression in the posterior plate; *Sarothromyia femoralis* var. *simplex* Ald. is an exception; buccal armature as in figs. 28 to 33; no accessory sclerites around hooks; pharyngeal sclerite large and flaring; dorsal cornua often larger than ventral cornua, and always deeply incised; ventral cornua often with clear window; ventral pharyngeal ridges sometimes present; posterior spiracular plates of two types; first, ear-shaped, peritreme open, button indistinct or absent, figs. 57, 64, 71, 78, 85; second, peritreme complete but weak, button distinct, figs. 70, 77 and 84; slits

in both cases elongate and subparallel; run dorsally or laterodorsally from button.

KEY TO SUBFAMILIES

Adults

1. Abdomen with three rows of shining black spots on second, third and fourth segments; arista pubescent; two or four presutural dorsocentrals; three humeral bristles present. *Wohlfahrtia* ..... **Sarcophaginae**
   Not with above combination of characters 2
2. Arista bare or lightly pubescent; two presutural dorsocentrals; scutellum with two pair of lateroscutellars; male genitalia generally not protuberant ..... **Miltogramminae**
   Arista long or short plumose; two to four presutural dorsocentrals; one to three pair of lateroscutellars; male genitalia may be protuberant (*Sarcophaga*) ..... **Sarcophaginae**

Third Instar Larvae

1. Posterior spiracular plates ear-shaped; peritreme open or greatly weakened ventrally at button; button may be present, fig. 57, but is generally indistinct or absent, figs. 64, 71, 78, 85 ..... **Sarcophaginae**
   Posterior spiracular plates lemon-shaped or ovoid; peritreme weak but complete; button generally distinct, figs. 70, 77, 84 ..... **Miltogramminae**

Subfamily **Miltogramminae**

There are twenty-four genera of this subfamily in North America; adults of representatives of eight of these and the larvae of three have been studied.

Adult.—Third antennal segment as long as wide to six times as long as wide; base of antenna often high and forward and frons horizontal; three or four frontoorbitals generally present.

Two notopleural, two postalar, and two presutural dorsocentrals present; wings as in fig. 114; apical cell may be closed; male genitalia usually not enlarged.

Third instar larva.—Body may be devoid of spines; posterior spiracles as in figs 70, 77, 84; buccal armature as in figs. 28, 29.

Subfamily **Sarcophaginae**

There are approximately thirteen genera of this subfamily in North America; adults and larvae of representatives of three have been studied.

Adult.—Third antennal segment one to three times as long as wide; arista plumose two-thirds distance to tip, pubescent in *Wohlfahrtia;* two or three frontoorbitals and four to six frontals present.

Two or three humerals, two to four notopleurals, and two postalars present; two to four presutural dorsocentrals; wing as in fig. 108; male genitalia may be large and protuberant, (*Sarcophaga*).

Third instar larva.—Posterior spiracular plates in depression except for *Sarothromyia;* button present in *Sarothromyia;* posterior spiracular plates as in figs. 57, 64, 71, 78, and 85; buccal armature as in figs. 20 to 33.

Superfamily **Oestroidea**

This superfamily, as has been previously noted, is not here treated in detail because of lack of larval material. All the flies generally placed in the Larvaevoridae, Oestridae, and Cuterebridae are included

here. The exact limits of the subdivisions of this superfamily are in doubt and its division into the Oestridae and Larvaevoridae is strictly tentative.

REFERENCES CITED

Aldrich, J. M. 1916. *Sarcophaga* and allies in North America. Thomas Say Found., LaFayette, Indiana. 301 pp. 16 pl.

Allen, H. W. 1926. North American species of two-winged flies belonging to the tribe Miltogrammini. Proc. U. S. Nat. Mus. 68 (art. 9, no. 2610): 1–106, 5 pl.

Bisset, G. A. 1938. Larvae and pupae of tachinids parasitizing *Pieris rapae* and *P. brassicae* L. Parasitology, 30: 111–122, illus.

Crampton, G. C. 1944. A comparative morphological study of the terminalia of male calyptrate cyclorrhaphous Diptera and their acalyptrate relatives. Bull. Brooklyn Ent. Soc., 39: 1–31, 54 figs.

Curran, C. H. 1934. The families and genera of North American Diptera. 512 pp., illus.

Girschner, E. 1893. Beitrag zur Systematik der Musciden. Berliner Ent. Zeitschr. 38: 297–312.

Hall, D. G., Jr. 1932. Biology of *Sarothromyia femoralis* var. *simplex* Aldrich (Diptera: Calliphoridae). Ann. Ent. Soc. Amer., 25: 641–647, 2 pls.

1948. The blowflies of North America. Thomas Say Found, LaFayette, Indiana. v+477 pp., 5 col. pl., 46 pl., 9 text figs.

Hewitt, C. G. 1912. *Fannia* (*Homalomyia*) *canicularis* Linn. and *F. scalaris* Fab. An account of the bionomics and the larvae of the flies and their relation to myiasis of the intestinal and urinary tracts. Parasitology, 5: 161–174, illus.

Huckett, H. C. 1936. A revision of connectant forms between Coenosian and Limnophorine genera occurring in North America. Jour. New York Ent. Soc., 44: 187–222, 5 pls.

Johannsen, O. A. 1935. Aquatic Diptera, Part II: Orthorrhapha, Brachycera and Cyclorrhapha. Cornell Univ. Agr. Exp. Sta. Mem., 177: 62 pp., illus.

Knipling, E. F., and **A. L. Brody.** 1940. Some taxonomic characters of cuterebrine (Diptera) larvae, with larval descriptions of two species from Georgia. Jour. Parasit., 26: 33–43, 2 pls.

Latreille, P. A. 1805. Histoire naturelle des crustaces et des insectes. Vol. 13: 1–432.

Linnaeus, C. von. 1758. Systema Naturae, ed. 10, 823 pp.

Macquart, J. 1834–35. Histoire naturelle des insectes diptéres (Suites a Buffon, ed. Roret) Paris, Roret. Vol. 1–2, 1288 pp., 24 pls.

Malloch, J. R. 1917. Key to the subfamilies of Anthomyiidae. Canadian Entom., 49: 599.

1919. The limits of the Dipterous group Calyptrata (Cyclorrhapha). Bull. Brooklyn Ent. Soc., 14: 111–112.

1923. A new character for differentiating the families of Muscoidea (Dipt.). Ent. News, 34: 57–58.

Meigen, J. G. 1800. Nouvelle classification des mouches á deux ailes (Diptera L.) d'apres un plan tout nouveau. Paris.

Meigen, J. W. 1803. Gattungs-Eintheilung der europaischen zweiflugligen Insekten. Illiger's Magazin f. Insekten, 2: 259–281.

Osten-Sacken, C. R. 1884. An essay of comparative chaetotaxy. Trans. Roy. Ent. Soc. London, 1884: 497–517.

Parker, R. R. 1914. Sarcophagidae of New England. Males of the genera *Ravinia* and *Boettcheria*. Proc. Boston Soc. Nat. Hist., 35: 1–77, illus.

1919. North American Sarcophagidae. Flies of the genus *Metoposarcophaga* Towns. Canadian Entom., 51: 154–158.

Robineau-Desvoidy, J. B. 1830. Essai sur les Myodaires, Paris. Vol. 2: 813 pp.

Séguy, E. 1923. Diptéres Anthomyides, Faune de France. Paul Lechevalier, Paris. 390 pp., illus.

1937. Diptera, family Muscidae. Genera Insectorum, 205: 595 pp., 9 pls.

Shannon, R. C. 1923. Genera of nearctic Calliphoridae, blowflies, with a revision of the Calliphorini. Insec. Inscitiae Mens., 11: 101–118.
1924. Notes on Calliphoridae. Insec. Inscitiae Mens., 12:14.
1926. Synopsis of American Calliphoridae (Diptera). Proc. Ent. Soc. Washington, 28(6): 115–139.
Siddons, L. B., and **D. N. Roy.** 1942. On the life history of *Synthesiomyia nudiseta* Van der Wulp (Diptera, Muscidae). A myiasis producing fly. Parasitology, 34: 239–245, illus.
Tate, P. 1939. The early stages of *Limnophora exurda* Pand. (Diptera, Anthomyidae). Parasitology, 31: 479–485, 11 figs.
Thompson, W. R. 1934. The tachinid parasites of wood lice. Parasitology, 26: 378–448, 8 pls., 5 figs.
Thomson, R. C. Muirhead. 1937. Observations on the biology and larvae of the Anthomyidae. Parasitology, 29: 273–358, 157 figs.
Townsend, C. H. T. 1892. The North American genera of the calyptrate Muscidae. Proc. Ent. Soc. Washington, 2: 89–100.
1914. Connectant forms between muscoid and anthomyoid flies. Ann. Ent. Soc. Amer., 7: 160–167.
1935–1942. Manual of Myiology, Vols. 1–12. C. Townsend and Filhos, Sao Paulo. 3736 pp., 84 pls.
Walker, E. M. 1937. The larval stages of *Wohlfahrtia vigil* (Walker). Jour. Parasit., 23: 163–174, 4 pls.
Westwood, J. C. 1840. Synopsis of the genera of British flies, *in* An introduction to the modern classification of insects. 2: 141–143.
Williston, S. W. 1908. Manual of North American Diptera, 3rd ed. James T. Hathaway Co., New Haven, Conn. 405 pp., illus.

LARVAE OF INSECTS. PART II. COLEOPTERA, DIPTERA, NEUROPTERA, SIPHONAPTERA, MECOPTERA, TRICHOPTERA, by ALVAH PETERSON. 416 pages, 104 plates. Lithoprinted, Edwards Brothers, Inc. 1951. Price, $7.00.

This part completes the first edition of the first comprehensive manual published on the larvae of the Nearctic species of insects, and consequently offers a laboratory text for the teaching of this important and increasingly popular subject. Part II is truly a continuation of Part I, which it follows closely in style and scope. The introductory material, therefore, is cut to a minimum.

The keys to the Coleoptera are based on those of A. W. Rymer Roberts rather than on the more recent ones of Böving and Craighead and of Van Emden. Those for the Diptera, especially the Cyclorrhapha, are inadequate, but represent, perhaps, as good as can be expected at the present time. The smaller holometabolous orders are treated quite briefly.

The illustrations are copious and good, and, as in Part I, each is accompanied by a concise description. There are quite a few typographical errors of a minor nature which we hope a second edition will correct. Some inconsistencies are evident; for example, in the citation of authors' names and in the use of the name Fungivoridae based on a Meigen 1800 name, whereas for the most part these names are not used.

Though copies arrived late, the reviewer and the students in his graduate class in larval taxonomy found this work quite effective for classroom use.—M. T. J.

THE IMMATURE STAGES OF AEDES INFIRMATUS DYAR AND KNAB WITH NOTES ON RELATED SPECIES

(Diptera: Culicidae)[1]

OSMOND P. BRELAND[2]
The University of Texas

INTRODUCTION

The mosquito, *Aedes infirmatus*, was described by Dyar and Knab (1906) only from larvae that had been collected at Baton Rouge, Louisiana. The original description was not a formal one, but the species was included in a key with other larvae; the features used in the key were considered to be of sufficient diagnostic value for a determination of the species. The larvae and adults were described in more detail later (Howard, Dyar and Knab, 1917, Vol. 4).

Aedes infirmatus belongs to a group which contains several very similar species. These include *Aedes scapularus* (Rondani) and *Aedes trivittatus* (Coquillett), species that also occur in the United States. Since these mosquitoes were described there has been considerable controversy relative to key features which may be used successfully to distinguish the three species.

Matheson (1944) distinguishes all three species on the bases of larvae, adult females and male genitalia. Recently, however, Gjullin (1946) has stated that the adult females of *infirmatus* and *scapularis* are not separable, while Carpenter, Middlekauf and Chamberlain (1946) do not distinguish *trivittatus* and *infirmatus* in their key using male genitalia. *Scapularis* does not occur in the area covered by the latter publication. Since one objective of this paper is a re-evaluation of the larval features that have been used for distinguishing the three species, these will be discussed later.

Aedes trivittatus is the most widely distributed in the United States of any of this group. It occurs in Southern Canada and generally over the Eastern half of the United States and as far west as Montana and Colorado (Carpenter *et al.*, 1946). *Aedes scapularis* is found in southern Texas and in Mexico, Central and South America (Matheson, 1944). *Aedes infirmatus* occurs in the southeastern states and as far west as Texas (Carpenter *et al.*, 1946). So far as could be determined, previous reports of *A. infirmatus* from Texas have been based on adult females collected from the southeastern part of the state. The present

[1]Supported by the University of Texas Research Institute.

[2]The writer wishes to express appreciation to Miss Grace Hewitt who made the drawings, Jay Buxton, Robert Hedeen and O. P. Wilkins who collected some of the specimens used in this study, and to Mr. George Menzies and Dr. Richard Eads of the Texas State Health Department who loaned specimens of *Aedes scapularis*.

paper thus reports for the first time the recovery of larvae, the features of which are much more distinct from *scapularis* than are the adult females.[3]

All three mosquitoes under consideration bite man readily during the day and may occasionally attain sufficient numbers to become a local problem in woodland areas (Matheson, 1944; Owen, 1937; Randolph and O'Neill, 1946).

The final decision relative to the actual status of *A. trivittatus*, *A. infirmatus* and *A. scapularis* must await additional study of large series of larvae and reared adults from known larvae. Such series are not available at the present time.

THE PRESENT STUDY

On October 28, 1949, a few days after a rain, several peculiar mosquito larvae were collected at Palmetto State Park, eight miles south of Luling, Texas. These specimens were noticeable with the unaided eye because they were somewhat bicolored. The head, dorsal abdominal segments and siphon were dark, while the remainder of the body was light. It should be noted that this contrasting coloration was not as obvious as had been previously reported for the larvae of another species (Breland, 1948). The larvae were tentatively determined as *Aedes infirmatus* and an attempt made to rear some of them to maturity. A high mortality resulted, but one female emerged which helped to confirm the identification. Several additional collections were attempted at later dates but no more larvae were recovered.

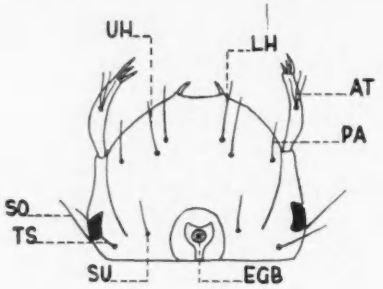
Approximately one month later, however, several female mosquitoes were on two occasions obtained while biting the collectors. Several species were involved including *Aedes infirmatus*, *A. trivittatus* and *Psorophora longipalpus* Roth. The mosquitoes were allowed to feed to repletion before they were captured; they were then confined in cages in the laboratory in an effort to procure egg deposition. Three dishes containing either moist dirt, moist filter paper or water were kept in each cage. The laboratory temperature varied from approximately 75° to 80° F. and moist towels were kept over the cages to maintain humidity.

Several females of *A. infirmatus* deposited a few eggs on the soil, but none were laid on the water or moist filter paper. Most of the eggs were laid in cracks and crevices in the dirt. The soil containing the eggs was allowed to dry for approximately a week after which it was flooded with pond water. Only one batch from a single female proved viable. Within fifteen minutes after flooding many larvae appeared, and some of these were isolated for study in individual staining dishes containing bits of *Elodea* leaves and algae. Small amounts of powdered brewer's yeast was added to the water surface daily. A second drying and flooding ten days later yielded additional specimens, but no more larvae were obtained although the soil was dried and flooded several times. Since no males were present in the cages, at least one female

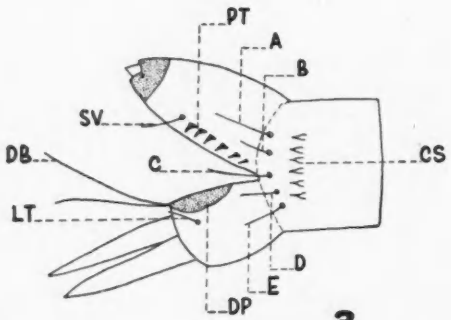
[3]Since this paper was submitted for publication, larvae of *A. infirmatus* have been reported from Texas. Mosquito News 10: 60–63, 1950.

had obviously been inseminated before receiving a blood meal from the collector. It is of course, not known whether or not previous blood meals had been taken.

The following descriptions of each larval instar are based upon a study of the larvae noted above. Structural details were obtained from freshly killed specimens and from larvae mounted on slides. It was found that an examination of unmounted specimens is especially



1



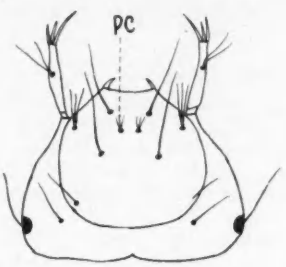
2

Aedes infirmatus Dyar and Knab, first larval instar. FIG. 1. Head. FIG. 2. Posterior abdominal segments.

ABBREVIATIONS

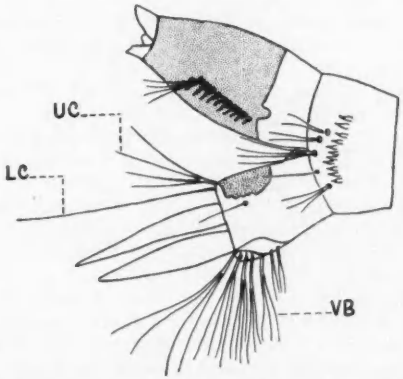
A—hair A (siphonal hair).
AT—antennal hair.
B—hair B.
C—hair C (subsiphonal hair).
CS—comb scales.
D—hair D.
DB—dorsal brush.
DP—dorsal plate or saddle.
E—hair E (anal hair.)
EGB—egg burster.
LH—lower head hair.
LT—lateral hair, anal segment.
Pa—preantennal hair.
PT—pecten.
SO—supraorbital hair.
SU—sutural hair.
SV—subventral tuft (siphonal hair).
TS—trans-sutural hair.
UH—upper head hair.

important for first instar larvae since this stage if mounted permanently often becomes distorted. There is considerable variation among the various instars in the number of branches in some of the hairs, and in the number and arrangement of certain other structures. However, those features present in the first instar are easily correlated with com-



3

4



5

Aedes infirmatus Dyar and Knab, second larval instar. FIG. 3. Head. FIG. 4. Representative comb scale. FIG. 5. Posterior abdominal segments.

ABBREVIATIONS

LC—lower caudal hair of dorsal brush.
PC—postclypeal hair (sometimes called preclypeal).
UC—upper caudal hair of dorsal brush.
VB—ventral brush.

parable structures of older larvae. Most structures are labeled in the drawings of the first instar (Figs. 1, 2) while those that are added in the second instar are labeled in figures 3 and 5.

No accurate observations were attempted relative to the specific length of each stadium. Larvae that emerged, however, averaged approximately 13 days from time of hatching to adult. In the descriptions to follow, those features are emphasized that are of greatest value in distinguishing instars.

THE IMMATURE STAGES

The Egg: The egg of *Aedes infirmatus* has been described and figured by Howard, Dyar and Knab (1912, Vol. 2). The eggs examined by the writer differed slightly from those described by these workers. One side of these eggs was more noticeably convex than described previously while the regular reticulations figured by the above authors could not be seen.

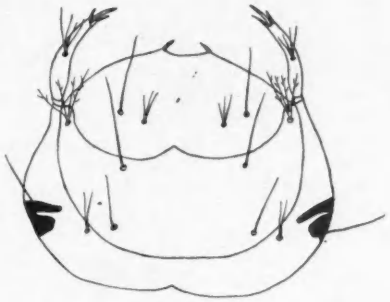
First Larval Instar (Figs. 1, 2): The egg burster (EGB) of this species is similar to that described for *Aedes trivittatus* (Abdel-Malek, 1949). It occurs in an oval depression and is a somewhat spoon-shaped plate with an anterior conical projection. All hairs on the head are single except the antennal hair (AT); this hair is two- or three-branched. The postclypeal hairs (PC, fig. 3) could not be seen in the specimens at hand. Even in older instars, however, these hairs are sometimes difficult to see and they may therefore have been present.

All hairs on the eighth abdominal segment are single, while there are four to six comb scales (CS) arranged in a single row. There are five or six pecten teeth (PT) while the subventral tuft (SV) is single. The individual pecten tooth differs from those found in later instars. It consists of a rather massive basal portion upon the distal edge of which are a number of spines. The spine nearest the distal end of the siphon is the longest, but one or more of the others are more than half its length. The basal part of the tooth is often roughly triangular in shape and is usually as long as or longer than the longest of the distal spines. The siphon is not chitinized except for a small area at the tip. The dorsal plate or saddle (DP) of the anal segment is represented by a small chitinized cap. The dorsal brush (DB) consists of two large hairs on each side which are sometimes so closely associated as to appear fused at the base. The lateral hair of the anal segment (LT) is single; the gills are longer than the anal segment and pointed. No ventral brush occurs in this stage.

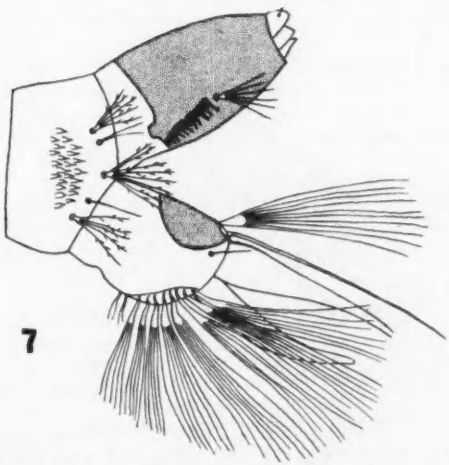
The bicolored pattern noted above becomes evident near the end of the first instar and is especially noticeable if the larvae are observed against a dark background. Also at this time, certain second larval features become visible through the skin. Some, such as the pecten teeth, are so much more noticeable than first instar structures that they may be easily interpreted as characteristic of the first instar.

Second Larval Instar (Figs. 3–4): Many of the hairs on the head of the second instar are similar to those of the first instar. The preantennal hairs have two to three branches. The postclypeal hairs (PC) are delicate two- to three-branched hairs. The egg burster, so characteristic of the first instar, is absent.

Aside from the absence of the egg burster, more obvious differences between the instars can be seen in the posterior region. A ventral brush (VB) occurs which consists of several hairs, most of which are three- or four-branched. The dorsal brush now consists of two parts,



6



7

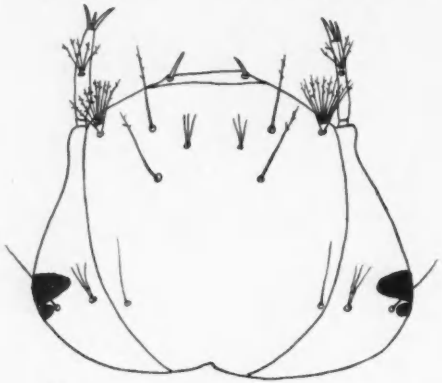
Aedes infirmatus Dyar and Knab, third larval instar. FIG. 6. Head. FIG. 7. Posterior abdominal segments.

upper and lower caudal hairs. The upper caudal (UC) on each side is composed of a tuft of hairs with three to five branches. A single long hair on each side makes up the lower caudals (LC).

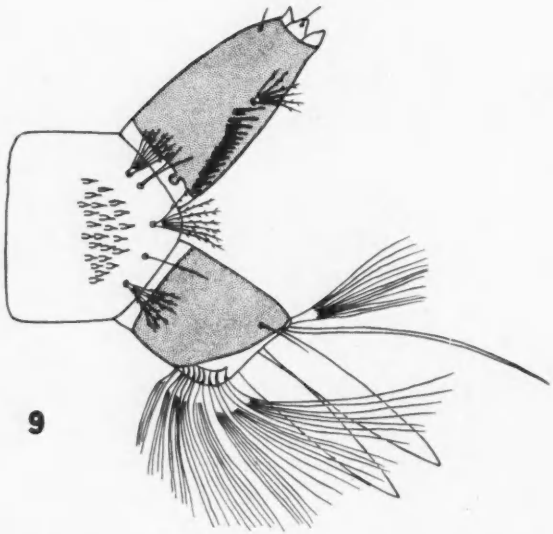
Several hairs on the eighth segments now have two or more branches. Hair A (A, Fig. 2) usually has two branches while three branches occur in an occasional specimen. Hair B(B, Fig. 2) consists of two branches.

Four to five branches occur in hair C, while hair D is single. The anal hair on hair E (E, Fig. 2) has three to four branches.

The comb is composed of nine to twelve scales on each side, and the scales are arranged in an irregular row across the segment. Under



8



9

Aedes infirmatus Dyar and Knab, fourth larval instar. FIG. 8. Head.
FIG. 9. Posterior abdominal segments.

high power, the individual comb scale (Fig. 4) is similar to that of later instars. The writer has not examined second stage larvae of *Aedes trivittatus*. However, a comparison of the comb scales of *Aedes infirmatus* with the drawing of a comb scale of the former species in a recent paper (Abdel-Malek, 1949), suggests that the two species can be distinguished even in the second instar on the basis of comb scale shape.

The siphon of this stage is chitinized for approximately two-thirds of its distal length. The subventral tuft has three to five branches. The individual pecten tooth is quite different from that of the first instar and resembles that found in later stages.

Third Larval Instar (Figs. 6, 7): Two eyes on each side are very evident in the third instar, and the members of each pair are often not in contact with each other. The anterior eyes, presumably represent the beginning of the eyes of the adult (Howard, Dyar and Knab, 1912, vol. I; Abdel-Malek, 1949). In some late second instars the larval eyes are partly divided which suggests that the anterior ones may be derived from the original larval eyes.

The comb scales on the eighth segment are now arranged in a definite patch, while some of the hairs are more noticeably barbed than in the second instars. The upper caudal tuft of the dorsal brush has 10 to 11 hairs in this stage, while most of the tufts of the ventral brush have six or seven.

Fourth Larval Instar (Figs. 8, 9): Most fourth instars can be easily distinguished from previous stages. The dorsal plate or saddle completely surrounds the anal segment in the fourth instar while this structure is only a cap on the dorsal posterior part of the segment in younger instars. In the specimens at hand, there is some variation in the length of the siphon. Most recent descriptions state that the siphon of the fourth instar is two and one-half times as long as wide. (Carpenter, *et al.*, 1946; Matheson, 1944.) This corresponds with all the writer's specimens except for two which were reared from eggs. In these larvae the length of the siphon is less than twice its width, but since the specimens were reared in the laboratory and mounted shortly after they attained fourth instar, they may have been somewhat abnormal.

COMPARISON OF FOURTH STAGE LARVAE

The fourth stage larvae of *Aedes infirmatus*, *scapularis* and *trivittatus* are very similar, and some workers in the past have considered two or more of these species inseparable as larvae. Individuals who have attempted to distinguish between the various species have used several criteria for this purpose. These have included the number of pecten teeth, the length of the siphon, the shape of individual comb scales and the relative pilosity of the bodies of the larvae. The writer does not have large enough series to take into account all possible variations that might be encountered, but a study of the specimens available has revealed certain facts which are suggestive. The larvae studied were collected from the following localities: *Aedes infirmatus*, near Luling, Texas; *Aedes scapularis*, Harlingen and San Benito, Texas; *Aedes trivittatus*, Junction, Texas.

Pilosity: The bodies of all three species of larvae are pilose to

some extent, and in many instances, the hairs can be seen with a compound microscope under low power magnification (*e.g.*, 100×). *Aedes scapularis* is the most pilose of the group and in mounted larvae at least, the hairs are quite noticeable. The writer could not discern any appreciable difference between *trivittatus* and *infirmatus* in this feature. This feature is a comparative one and is thus of doubtful value in distinguishing the larvae.

Comb Scale Shape: Aedes scapularis can be easily distinguished from *trivittatus* and *infirmatus* on the basis of the shape of the individual comb scales. Each comb scale of *scapularis* is rounded at the end with spinules of approximately equal length (Fig. 12). Under low power magnification, the comb scales of *infirmatus* and *trivittatus* appear

Representative comb scales of *Aedes* larvae. FIG. 10. *Aedes infirmatus* Dyar and Knab. FIG. 11. *Aedes trivittatus* (Coquillett). FIG. 12. *Aedes scapularis* (Rondani).

thorn-shaped. At a higher magnification (*e.g.*, 440× to 880×) it can be seen that in both species there is a central spine with somewhat smaller lateral spines. The central spine of *infirmatus* is usually about twice the length and three or four times as broad as the lateral spinules (Fig. 10). In *trivittatus* the central spine is only about twice the width and only slightly longer than the lateral spines (Fig. 11). There is, however, some variation and since the feature is a comparative one, the two species of larvae are sometimes difficult to separate on this basis alone.

Other Characteristics: Length of siphon and number of pecten teeth were not found to be reliable features for distinguishing these three species of larvae. One additional difference was discovered, however, which was constant in all specimens studied by the writer. Hair B of the anal segment (B, Fig. 2) was double in all larvae of *infirmatus* available for study, while in *trivittatus* and *scapularis* larvae this hair was single. This feature is much easier to distinguish in *infirmatus* and *trivittatus* than are comb scale differences.

Carpenter, Middlekauf and Chamberlain (1946) do not discuss this possible difference between *infirmatus* and *trivittatus*. However, these workers do show this distinction in their drawings of the larvae, indicating that the differences in their material were constant enough to have been noticed. If large series from different localities demonstrate that the distinction is a constant one, *trivittatus* and *infirmatus* larvae will be relatively easy to separate in the future.

SUMMARY AND CONCLUSIONS

1. The eggs and larval stages of the mosquito, *Aedes infirmatus* Dyar and Knab, have been described. The eggs were deposited in the laboratory by a female collected in nature, and the descriptions of the instars based upon individually reared larvae obtained from the eggs.

2. A study has been made of the fourth larval instar of *Aedes infirmatus* Dyar and Knab, *Aedes trivittatus* (Coq.) and *Aedes scapularis* (Rondani) with the view of re-evaluation of the features previously used for the separation of the three. The series used were small and consequently conclusions must be considered as tentative. However, certain suggestions based on the material at hand, are noted below.

3. Of those features used in the past to determine these larvae, the shape of the comb scales was the only one found to be partially reliable.

4. Larvae of *Aedes scapularis* can be easily distinguished from those of *A. infirmatus* and *A. trivittatus* on the basis of differences in shapes of comb scales.

5. The larvae of *A. infirmatus* and *A. trivittatus* are often difficult to distinguish on the basis of comb scale shape alone. Hair B of the eighth abdominal segment is different in all specimens examined by the writer. In *A. trivittatus* the hair is single, while in *A. infirmatus* it is double. This distinction, if found to be constant in large series from different localities, should cause the determination of these larvae to be a relatively easy matter.

LITERATURE CITED

Abdel-Malek, Albert. 1949. A study of the morphology of the immature stages of *Aedes trivittatus* (Coquillett) (Diptera: Culicidae). Ann. Ent. Soc. Amer., 42: 19–37.

Breland, Osmond P. 1948. Some bicolored mosquito larvae. Journal Kansas Ent. Soc., 21: 120–121.

Carpenter, Stanley J., Middlekauf, Woodrow W., and **Chamberlain, Roy W.** 1946. The mosquitoes of the southern United States east of Oklahoma and Texas. The University Press, Notre Dame, Ind.

Dyar, Harrison G., and **Knab, Frederick.** 1906. The larvae of the Culicidae classified as independent organisms. Journal New York Ent. Soc., 14: 169–230.

Gjullin, C. M. 1946. A key to the *Aedes* females of America north of Mexico (Diptera, Culicidae). Proc. Ent. Soc. Washington, 48: 215–236.

Howard, Leland O., Dyar, Harrison G., and **Knab, Frederick.** 1912–1917. The mosquitoes of North and Central America and the West Indies. Carnegie Inst. Washington, Pub. 159: 4 Vols.

Matheson, Robert. 1944. Handbook of the mosquitoes of North America, Second Ed. Comstock Pub. Co., Ithaca, N. Y.

Owen, William B. 1937. The mosquitoes of Minnesota with special reference to their biologies. Univ. of Minnesota Agric. Exp. Sta. Tech. Bull. 126.

Randolph, Neal M., and **O'Neill, Kelly.** 1944. The Mosquitoes of Texas. Texas State Health Department, Austin.

THE EFFECT OF CONCENTRATION, TEMPERATURE, AND WASHING ON THE TIME OF APPEARANCE OF DDT-INDUCED TRAINS IN SENSORY FIBERS OF THE COCKROACH[1]

KENNETH D. ROEDER AND ELIZABETH A. WEIANT[2]
Department of Biology, Tufts College,
Medford, Mass.

The observations that DDT causes spontaneous twitching of amputated legs (Yeager and Munson, 1945), and impulse trains in sensory fibers from the campaniform organs of the cockroach (Roeder and Weiant, 1945, 1948), and in motor fibers of Crustacea (Welsh and Gordon, 1947), all suggest that DDT has an unstabilizing action on irritable tissue in arthropods. Gordon and Welsh (1948) conclude that DDT may interfere with the normal stabilizing action of calcium at the axon surface.

In studies designed to determine the site of action of DDT in the cockroach, *Periplaneta americana*, it was noted that a definite relation existed between the concentration of DDT suspension applied and the time of appearance of impulse trains in afferent nerve fibers originating in the Campiniform organs of the trochanter (Roeder and Weiant, 1945, 1948). A further study of this concentration-time relation is reported below in the hope that it may reveal something of the process by which DDT penetrates or attaches itself to the neuronal surface.

METHOD

The methods have been described in a previous paper (Roeder and Weiant, 1948). Electrical activity from sense organs in the cockroach leg was detected at the base of the crural nerve by means of silver electrodes connected to a Grass P3 amplifier, cathode-ray oscilloscope and loud-speaker. In most of the experiments a single injection of DDT suspension in saline was made by means of a syringe and No. 27 needle through the cut end of the tibia. Unless the suspension could be forced completely through the leg so that it appeared at the incision near the metathoracic ganglion, the preparation was discarded. The amount of DDT in the suspensions was expressed in parts (by weight) per million parts of saline. Saline suspensions of DDT were prepared by dissolving DDT in ethanol or triethylene glycol to produce a 1% solution. One cc of this solution was squirted rapidly through a No. 27 needle into 100 cc of insect saline. The faintly milky suspension of

[1]The work described in this paper was done under contract between the Medical Division, Chemical Corps, U. S. Army, and Tufts College. Under terms of this contract the Chemical Corps neither restricts nor is responsible for the opinions or conclusions of the authors.

[2]The authors wish to acknowledge the able assistance of Dr. Donald H. Osterberg of Tufts College Medical School in connection with measurements of the effect of temperature on the time of onset of DDT-induced impulse trains.

100 ppm. DDT appeared to be stable for about 10 hours, and was used for further dilutions.

AFFERENT IMPULSES IN THE CRURAL NERVE

The origin and nature of electrical activity in the crural nerve of the cockroach was first described by Pringle (1938). This nerve appears to contain fibers from most of the sensory structures (spines, campaniform, and hair sensilla) of the leg, and a few motor fibers supplying muscles of the coxa. If efferent impulses in motor fibers are eliminated by destruction of the ganglion, a series of afferent impulses originating from sense organs in the leg may be recorded from electrodes placed below the crural nerve before it enters the metathoracic ganglion.

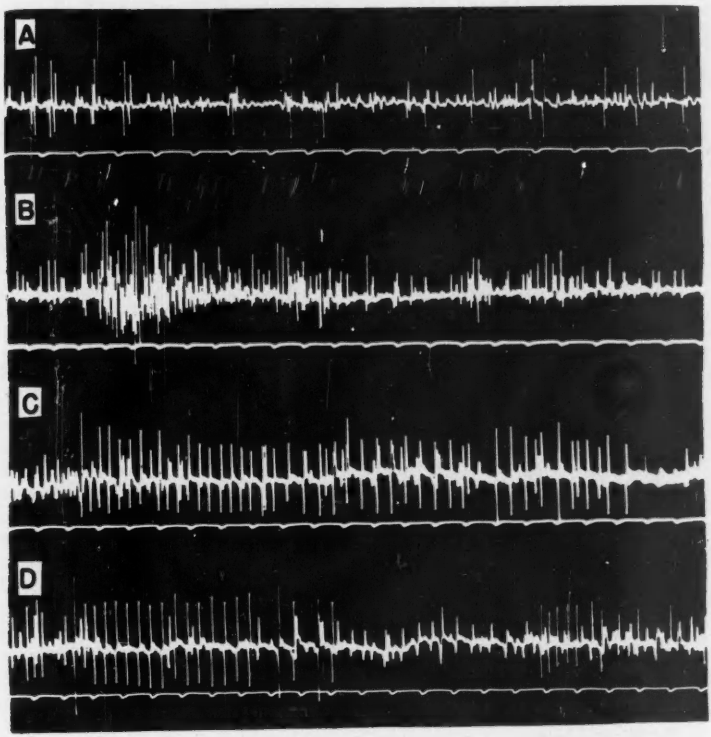


FIG. 1. Afferent spike potentials originating in campaniform sensory cells and recorded from electrodes placed on the crural nerve of the cockroach. The lower trace in each record is deflected at 0.01 second intervals. All records obtained from the same preparation. A. Basal activity (leg motionless). B. Burst of impulses elicited by light pressure on the trochanter. C. Five minutes after injection of DDT suspension through the leg. Train of impulses in a single fiber. D. Two minutes later. Impulse trains in several fibers as revealed by the different spike heights.

Amputation of the leg below the trochanter eliminates many of the sense organs, leaving a simplified pattern of impulses which originate mainly in sensory cells of the campaniform organ in the trochanter. A record typical of the preparation at this stage is shown in fig. 1A. While the leg is motionless there is a relatively steady but asynchronous series of spikes, each spike being due to activity in a single fiber. Analysis of longer records indicates that each fiber discharges rhythmically at rates of five to one hundred times per second. A number of fibers may be active, each discharging at its own frequency. Slight mechanical pressure on the trochanter or bending of coxo-trochantinal joint causes a brief high frequency burst of impulses (Fig. 1 B) which appears to be recruited both from fibers previously active and from others which were inactive before the stimulus.

After exposure of the tissues within the trochanter to DDT the pattern of impulses in the crural nerve changes in a highly characteristic fashion. Regularly recurring single spikes in single fibers are replaced by recurring trains of spikes, during which each fiber discharges repetitively at rates as high as 400 per second (fig. 1 C). Each high frequency train may last for 0.02 to 0.5 second and usually repeats at regular intervals as is the case with single spikes in the untreated preparation. Repeating impulse trains of this type may recur independently in several fibers (fig. 1 D), and will continue as long as the preparation remains viable. The appearance of impulse trains is readily detected as a recurrent musical note if the amplified electrical activity is fed into a loud-speaker, and served as the criterion of DDT action in the following observations. Both single spikes and trains apparently originate in the sensory cell-bodies of the campaniform organ, since both normal activity and DDT-induced impulse trains disappear following destruction of the sensory region in the trochanter.

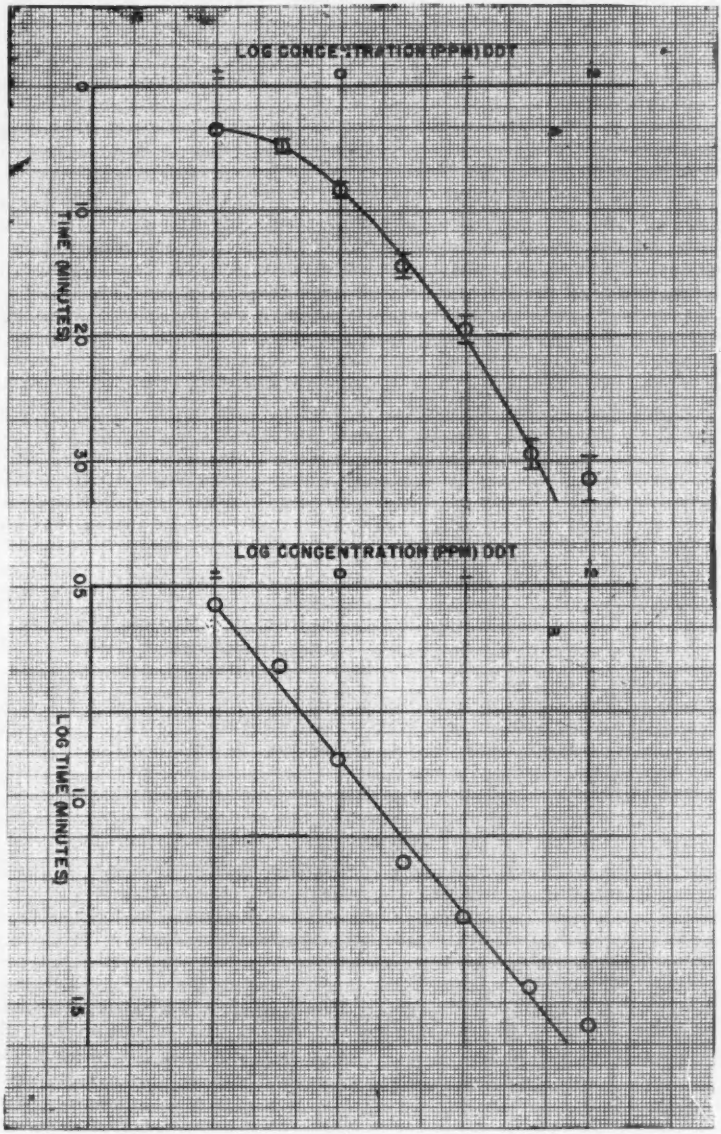
TIME OF ONSET AND CONCENTRATION OF DDT

In the course of observations to determine the site of action of DDT in the cockroach it was noted that trains of impulses appeared in afferent fibers of the crural nerve at a relatively constant time interval following injection of DDT suspension through the leg. If the suspension contained 10.0 to 100.0 ppm. DDT, impulse trains appeared within one minute. With lower concentrations the number and intensity of the trains appeared to be unchanged, though their appearance was delayed to a maximum of 30 to 40 minutes following 0.01 ppm. DDT, the lowest concentration used. Determinations of this time interval with DDT concentrations from 0.01 to 10.0 ppm. were made on 113 crural nerve preparations, and the average times at each concentration are given in figure 2. In figure 2 concentration is expressed

---

EXPLANATION OF FIGURE II

FIG. 2. The relation between concentration of DDT in a suspension injected through the leg of the cockroach, and the time appearance of impulse trains in afferent fibers of the crural nerve. Each point is the mean of a number of observations at a selected concentration, and the standard error of each mean is indicated by the double T. A: The vertical axis (concentration) is logarithmic, while the horizontal acis (time of onset) is linear. B: Both axes are logarithmic.


LOG CONCENTRATION (PPM) DDT
TIME (MINUTES)
0
10
20
30
LOG CONCENTRATION (PPM) DDT
LOG TIME (MINUTES)
0.5
1.0
1.5

in logarithmic units, while the time axis is linear; if both axes are logarithmic (fig. 2 B) a linear relation exists between the concentration of DDT applied and the time of onset of trains. A few observations with dibrom and dimethoxyphenyl analogs of DDT showed that a similar concentration time of onset relation exists with these substances, though the dibrom analog acts more slowly and the dimethoxy analog acts more rapidly than DDT. It should be said that there was considerable variation in individual determinations, and the standard error of the mean represented by each point is indicated by a vertical line. The only sharp criterion was the initial impulse train in a single fiber of the compound crural nerve, so that the effect of DDT on the most sensitive neurone in the leg was being measured. This circumstance might be expected to cause considerable variation from preparation to preparation, but the appearance of the first train as determined by the musical note in the loud-speaker was such a precise criterion that it was used in preference to some measure of the average number of neurones affected.

The true solubility of DDT in aqueous solutions is not known, but it is probably less than 0.1 ppm. Since the time-concentration relation described above was obtained with suspensions containing 0.01 to 10.0 ppm. DDT, the physiological effect of DDT must be due at least in part to the action of suspended particles rather than to the small amount of DDT in true solution. At the time of the single injection the campaniform neurones must become immediately surrounded by a certain number of DDT particles. This initiates a progressive change in neurone stability which terminates in repetitive autoexcitation. The velocity of this change is a function of the number of DDT particles brought into contact with the neurone surface.

TIME AND ONSET OF TEMPERATURE

The observations recorded in figure 2 were made at room temperature. It was felt that the nature of the progressive change initiated by the arrival of DDT in the vicinity of the neurones might be better understood if its temperature coefficient were known.

The electrodes and preparation were enclosed in a thermostatically controlled cabinet which could be held at any temperature between 10° C. and 35° C. The cabinet had a glass top, and necessary adjustments were made through portholes and observed through a binocular microscope mounted above the cabinet. In order to test the effect of temperature on time of onset of trains, a concentration of 1.0 ppm. DDT was chosen. This normally produced trains in 7 to 9 minutes at room temperature (fig. 2), and any significant deviations from this time of onset could readily be detected.

The preparation was mounted and allowed to reach the temperature within the cabinet, which also contained a syringe filled with a suspension of DDT. After 30 minutes the suspension was injected through the leg by inserting the hands through port holes in the sides of the cabinet. Approximately eighty preparations were tested at six selected temperatures between 10° and 30° C. The individual times of onset of trains were more variable than those obtained without temperature control, a condition probably due to the difficulties of handling the

preparation within the cabinet. The average times plotted against temperature (fig. 3) indicate that the latter has little or no effect on the time of onset of impulse trains. Though there is a significant lengthening of the time of onset below 12° C. where it took almost twice as long for the trains to appear, there is no indication that the temperature coefficient of the process responsible for the delay between application and effect differs greatly from 1.0 when the experiment is carried out at temperatures greater than 12° C.

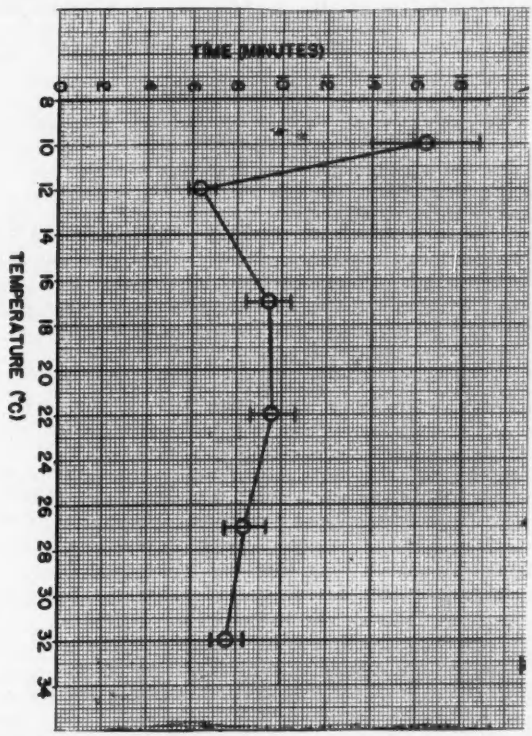


FIG. 3. The relation between the time of appearance of impulse trains in the crural nerve following a single injection of suspension containing 1.0 ppm. DDT, and the temperature of the preparation. A number of observations were made at each temperature selected, and the standard error of each mean is indicated by the double T.

WASHING WITH SALINE FOLLOWING DDT APPLICATION

The previous observation suggests the possibility that the time between the injection of DDT and the appearance of the first trains is occupied by a physical process such as progressive accumulation or

solution of DDT at the surface of the nerve cells. The attainment of a critical concentration would be a function of the density of particles in the immediate neighborhood or in actual contact with the neurone surface. In this case it should be possible to reduce the concentration of DDT particles in the vicinity of the neurones by washing with saline, thereby lengthening the interval before the appearance of trains.

To test this possibility, a suspension containing 0.3 ppm. DDT was injected into a series of legs in the manner described above. This concentration ordinarily produces trains in 17 minutes (fig. 2), and any lengthening of this interval by washing should be quite noticeable. At the same time the interval is sufficiently long to permit adequate

TABLE I

EFFECT OF WASHING UPON THE TIME OF ONSET OF IMPULSE TRAINS PRODUCED BY A SINGLE INJECTION OF 0.3 PPM. DDT

Time in minutes until the appearance of typical trains.

CONTROL NO WASHING	INTERVAL FOLLOWING DDT INJECTION BEFORE WASHING			
	1 minute	2 minutes	3 minutes	4 minutes
21	10	13	13	8
21	8	19	.....	9
14	15	.....	.....	16
.....	23	26	27	17
14	16	17	15	13
13	18	28	15	23
20	12	7	25	24
22	27	10	17	11
19	.....	.....	.....	.....
.....	.....	.....	.....	.....
16	.....	.....	.....	.....
10	.....	.....	.....	.....
Av. 17.0	15.9	17.1	18.6	15.1

flushing of the leg with saline. Following the injection of DDT, repeated washing with saline was begun at 1, 2, 3, or 4 minutes after the single injection of DDT suspension, while some preparations were not washed. Washing was carried out by flushing saline through the leg in the same manner in which the DDT had been introduced. The saline was observed to pass completely through the leg, and flushing was repeated several times so that any free DDT particles must have been removed or greatly diluted. The results of this procedure are given in Table I, which shows that washing as soon as one minute after DDT injection had no effect on the time of onset of trains. Thus DDT particles destined to cause the appearance of trains in an average time of 17 minutes must be bound at the neuronal surface within 1 minute and cannot be removed mechanically by saline passing over the same route.

CONCLUSIONS

A single application of DDT suspension to tissues in the leg of the cockroach causes repetitive trains of impulses to appear in afferent fibers of the crural nerve after a definite time interval. The fact that the logarithm of this time interval is proportional to the logarithm of the density of DDT particles originally applied, and that the temperature coefficient is close to unity indicates that the process which takes place during this time is a physical one. However, frequent washing indicates that absorption or fixation of DDT particles by tissues of the leg is complete within one minute after application of a concentration which normally takes seventeen minutes to unstabilize the nerve cells. Therefore, binding of DDT from suspensions coming into direct contact with sensory neurones cannot be the progressive process which occupies the time interval between application and the appearance of trains.

The only conclusion on the evidence available is that two processes are concerned. The first of these is completed within one minute and consists of fixation or adsorption of DDT particles at the surface of the sensory neurone in contact with the intercellular medium. The second process may consist of solution of DDT in a lipoid film below the neurone surface. The time required for the development of a critical (unstabilizing) concentration in this lipoid layer must be a function of the amount of DDT originally bound at the outer surface of the neurone. When examined from a physicochemical viewpoint, this conclusion implies an apparent paradox. The demonstrated relation between the density of DDT particles and the velocity of the process climaxed by impulse trains implies the attainment of an equilibrium between the suspension and the neurone. On the other hand, the observation that immediate dilution or removal of DDT from the vicinity of the neurone by washing is without effect on the velocity of the process leading to trains, implies that the arrival of DDT initiates an immediate and irreversible change at the neurone surface.

SUMMARY

1. Oscillographic recording reveals that trains of impulses appear in afferent fibers of the crural nerve of the cockroach only when a definite period of time has elapsed since the injection of DDT through the leg.

2. The log time of onset of trains is inversely proportional to the log concentration of DDT particles in the suspension.

3. The time of onset of trains after injection of a suspension containing 1.0 ppm. DDT is unaffected by temperature between 12° C. and 32° C., suggesting that the interval is occupied by a physical process.

4. The effects of injection of 0.3 ppm. DDT could not be removed by washing repeatedly with saline, though the trains of impulses did not appear for 17 minutes.

5. It is suggested that DDT is immediately bound at the surface of the sensory neurones, the time interval between application and the appearance of impulse trains being occupied by solution of DDT in a

lipoid layer below the neurone surface. The attainment of a critical concentration at this lipoid layer is indicated by the appearance of impulse trains in the afferent fibers.

LITERATURE CITED

Gordon, H., and **J. H. Welsh.** 1948. The role of ions in axon surface reactions to toxic organic compounds. Jour. Cell. and Comp. Physiol., 31: 395–419.

Pringle, J. W. S. 1938. Proprioception in insects. II. The action of the campaniform sensilla on the legs. Jour. Exper. Biol., 15: 114–131.

Roeder, K. D., and **E. A. Weiant.** 1945. The site of action of DDT in the cockroach. Science, 103: 304–306.

Roeder, K. D., and **E. A. Weiant.** 1948. The effect of DDT on sensory and motor structures in the cockroach leg. Jour. Cell. and Comp. Physiol., 32: 175–186.

Welsh, J. H., and **H. Gordon.** 1947. The mode of action of certain insecticides on the arthropod nerve axone. Jour. Cell. and Comp. Physiol., 30: 147–172.

Yeager, J. F., and **S. C. Munson.** 1945. Physiological evidence of a site of action of DDT in an insect. Science, 102: 305–307.

THE NATURALISTS' DIRECTORY, 36th edition. The Cassino Press, Salem, Mass. 262 pages. Price, $3.00.

First published in 1876, this directory has appeared with revisions at two- to three-year intervals. In its present form it contains names and addresses and fields of special interests of naturalists from all parts of the world. In addition, there is a list of Natural History Museums, Scientific Societies, and Scientific periodicals.

This directory is a very useful medium for bringing together naturalists interested in similar fields of study. It lacks something in the way of completeness and accuracy of addresses, but anyone who has had experience in keeping membership lists up-to-date will realize what a tremendous job that can be. The task of the editors of the *Natrualists' Directory* is, of course, a much greater one. The usefulness of the *Directory* will be increased if individual naturalists will cooperate in attempting to correct errors or fill omissions known to them.—M. T. J.

STUDIES ON THE SEASONAL PREVALENCE AND DISPERSAL OF THE EGYPTIAN HOUSEFLY[1,2]

I. The Adult Flies

R. T. HOLWAY, LCDR, MSC, USN, W. A. MITCHELL, HMC, USN, AND ABDEL AZIZ SALAH

United States Naval Medical Research Unit No. 3,
Cairo, Egypt

This is the first of two parts of a report on field studies of the seasonal abundance and local dispersal of the housefly in Egyptian villages. Part I considers the adult fly population while Part II takes up the problem of the larvae and the types and distribution of their breeding areas.

The designation of the common Egyptian housefly accepted by Sabrosky (*in litt.*), namely, *Musca domestica vicina* Macq. (including form *nebulo*) is followed in this report. The work of Hafez (1941) indicates that other species of *Musca* with different preferences for breeding material are present in Egypt but he states that *M. d. vicina* comprises the great majority of the house-frequenting flies. Over 97% of thirteen hundred and ninety-six flies trapped and reared from various types of breeding materials in two Egyptian villages by the authors in 1948–1949 were identified by C. W. Sabrosky of the United States National Museum as *M. domestica vicina* Macq. There appears to be general agreement that a very high percentage of the houseflies are *vicina* and no attempt has been made here to separate the small numbers of other species which may be present.

Four typical villages in Giza Province were selected for the study of various aspects of the fly problem. The most prominent characteristic of these typical Egyptian peasant villages is the way in which the private houses are concentrated in a relatively small area with common walls and contiguous roofs in an almost honeycomb-like proximity. Blocks of many houses are constructed back to back and open only on one side into narrow alleys or streets. Figure 1 shows the relative size and arrangement of the four experimental villages.

The experimental villages are separated from other villages and from each other by at least 0.4 miles. Moneeb and Wali Bey are 0.4 miles apart and Ashtar and Harania at 0.7 and 1.4 miles from the next nearest village, respectively. The areas between villages is almost completely open farm land. The built-up area is approximately only seven acres in Moneeb, Wali Bey and Harania, and twenty acres in Ashtar. From two hundred to five hundred family houses may be concentrated in these limited areas.

---

[1]The opinions expressed in this article are those of the authors and are not to be construed as reflecting the views of the Navy Department.

[2]The authors wish to express their gratitude for the assistance received during the course of this work from the staff of the U. S. Naval Medical Research Unit No. 3.

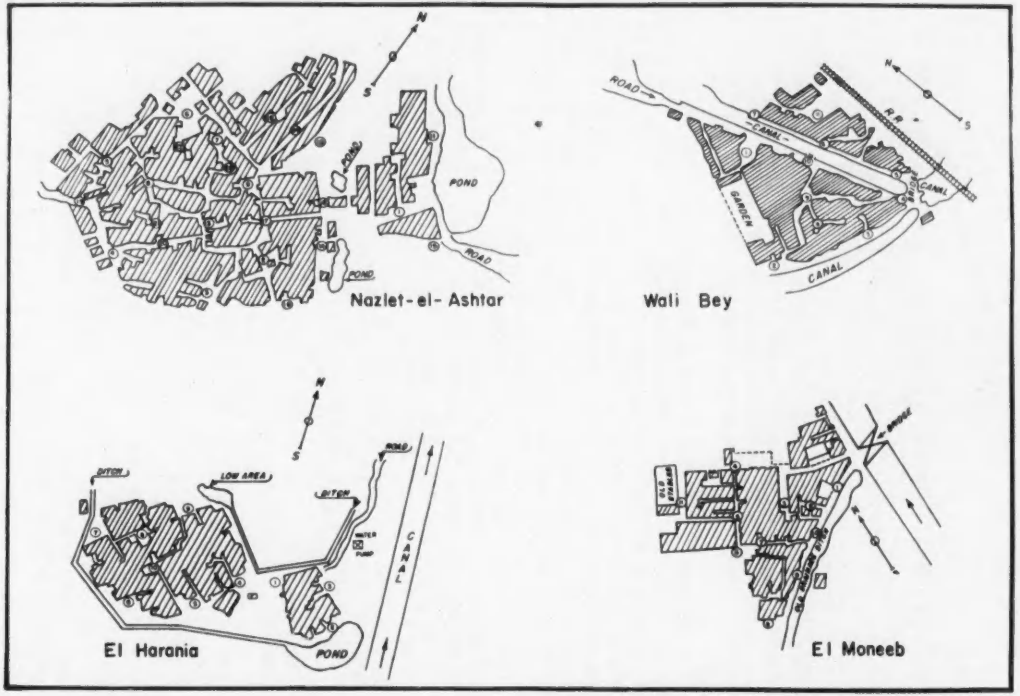


FIG. 1. Experimental villages in Giza Province showing concentration of houses in small areas. Scale, 1 inch = 690 ft.

METHODS

The seasonal and diurnal population changes reported herein are based upon data collected by use of the fly grill method for estimating relative fly densities. The procedures and principles suggested by Scudder (1947) were followed as closely as possible except where certain modifications seemed desirable because of local conditions.

A basic characteristic of the grill count method pointed out by Scudder is the unsatisfactory nature of random counts. The fly habit of concentrating at a relatively few highly attractive foci means that random placement of the grill will result in many zero counts and few high counts, with a resultant biased mean. Therefore the grill is used to measure the relative size of fly populations at points where flies are concentrated. Although this procedure complicates or eliminates the application of statistical analysis and introduces another source of error in the form of the inspectors' activity in finding concentration foci, a practical justification for its use is found in the results obtained.

Attraction centers are of basic importance in fly density studies by the grill method. Fly concentrations are seldom found in the open fields as the greatest attraction centers occur in the densely populated villages. The common attraction foci outside of houses are human stools, latrine-dumps, dates (in season), discarded sugar cane, small or large collections of wastes, particularly where water has been dumped and the ground is slightly moist, compost piles, (when fresh and attractive materials are present), slaughtering sites, food, and mucous secretions of very young children. All these types of attraction centers are usually found scattered throughout the narrow alleys, around the perimeter, and in the occasional open squares of the village.

Strong attraction foci are even more common inside houses. These are found in shops, particularly meat and milk processing establishments, cafes and general shops, where candy, sugar and other attractive materials are sold. Also inside the houses, animal rooms and food collections, especially sugar cane and dates, provide attractive foci.

The grill used was 30″ x 32″ and consisted of ¾″ wooden strips nailed ¾″ apart on a supporting frame. The grill was placed at the center of a fly concentration and the flies in the vicinity were gently disturbed to start them circulating around the grill. The count was made as rapidly as possible after a wait of 30 seconds. At first three counts were made at each placement and the highest count recorded was used but after summarizing results over a period of several months it was found that the village daily averages based on first, second and third counts were highest for the first count on seventy-six out of ninety-eight days. Furthermore, in the cases where second and third counts were highest the difference was very slight while the first counts were often greatly in excess of the others. Consequently second and third counts were omitted.

The theory of the grill method as proposed by Scudder calls for the use of a function of both the number of maxima and the size of each count. A constant number of the highest counts in a given block, for example, were selected and the arithmetic mean of these maximal counts was considered as the fly index for the area. In applying this method to local conditions, an Egyptian village has been considered as roughly the equivalent of a city block.

As counts were to be taken at points of highest concentrations of flies the selection of these points obviously would affect results to a very great extent. Variation in the location of attraction foci is considerable so that the use of fixed stations would mean that a great many very low counts would be obtained. Therefore general areas or zones were set up throughout the village and the count for each zone was taken at a point where fly concentration appeared to be the highest.

There was no valid basis for determining the number of zones per village in which a count should be taken to provide a daily index. The most important consideration was to cover the village adequately so that the maximum foci would be detected and counted. The effect which the use of maximum counts will have on a weekly index (four days per week) is shown in figure 2 where curves are plotted on the basis

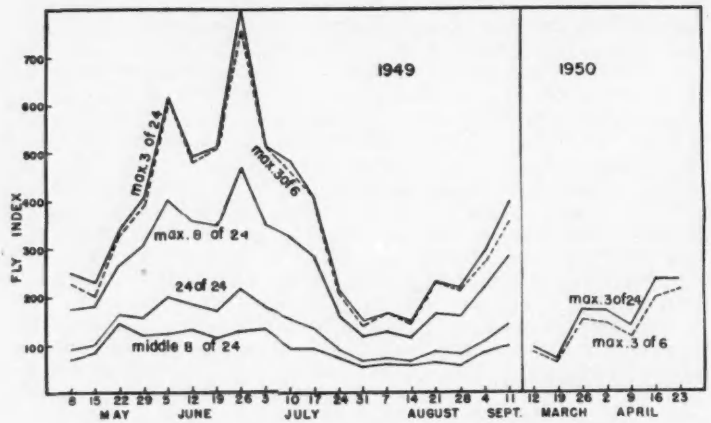


FIG. 2. Effect of the number of zones used in computing weekly fly index at Ashtar on the seasonal curve.

of twenty-four zones in the village of Ashtar. The three highest zones, the eight highest, the middle eight and the average of all twenty-four zones are shown. All curves show similar relative trends with peaks and depressions at approximately the same date except for that of the middle eight which obviously is of no value for determining relative density levels. The maximum three give a more sensitive reaction to changes in fly density.

It is desirable, therefore, to obtain a small number of the highest counts obtainable in the village with a minimum of time and effort. One method would be to take counts in a large number of zones so that most of the points of maximum density would surely be detected and the highest selected from the total. Another possibility is to select no zones but merely to roam about the village taking counts where there seemed to be exceptionally high concentrations. Either system involves considerable waste of time and in the latter case an even greater reliance on the judgment and integrity of the checker.

A large number of zones were used during 1949 to be sure that the villages were adequately covered and counts were made at both inside and outside locations for each zone. A summary of the data indicates that high count zones tend to remain high and low count zones to remain low quite consistently. Table I shows the frequency with which the same zones appeared within the highest six at Ashtar on the basis of monthly averages at inside locations for thirteen months. If six zones (Numbers 4–5–7–14–21–22 at Ashtar) are selected from the total of 14 (later 24) on the basis of consistently high inside counts it is evident from the table that at least three of these will appear among the highest six during every month.

It can be seen from figure 2 that it is unnecessary to make counts in all zones or to survey the entire village on every check day to obtain

TABLE I

FREQUENCY WITH WHICH HIGH COUNT ZONES REMAINED HIGH FOR INSIDE COUNTS FOR 13 MONTHS DURING 1948–1949 AT ASHTAR

	Zone Number												
	Sept.	Oct.	Nov.	Dec.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.
1st Highest Zone...	*5*	*5*	7	12	*14*	*14*	*14*	7	*5*	*5*	*5*	*5*	*21*
2nd Highest Zone...	*4*	7	6	*5*	12	*22*	*22*	*14*	*14*	*4*	*21*	*21*	*5*
3rd Highest Zone...	*14*	*4*	*4*	*4*	*4*	23	7	*5*	7	7	12	7	*4*
4th Highest Zone...	7	6	*5*	6	*5*	2	6	*22*	*4*	*22*	*4*	*4*	12
5th Highest Zone...	6	*14*	*14*	*14*	6	7	*4*	*21*	*22*	*21*	2	12	*14*
6th Highest Zone...	10	10	10	7	2	6	*5*	*4*	*21*	2	7	*14*	2

Zones selected as most likely to occur within the highest six (4–5–7–14–21–22) are underlined.

the desired number of maximum counts once the zones of greatest concentration are known. If only six zones had been counted from May to September instead of the actual twenty-four, the maximum three used for the village index would have given approximately the same relative weekly curve inasmuch as all of these three occurred consistently within the six highest zones. Even a year later there is only slight deviation when only the six originally selected zones are used instead of the total twenty-four as shown by the 1950 portion of the graph in figure 2. If necessary periodic rechecks of the entire village could be made to determine any changes in maximum zones.

Outside counts do not show the same consistency, which would be expected, since the zones were selected on the basis of inside high counts and, furthermore, outside attraction foci are more often of a temporary nature. A very attractive milk or meat shop, for example, is a constant and dependable fly concentration center whereas many outside attraction centers such as human stools are temporary foci. However, if for any reason outside relative density changes are of particular interest it will usually be possible to select six to eight zones

from the high outside counts which will consistently contain the three maxima.

DIURNAL VARIATIONS

A strong tendency for flies to move inside of houses with increasing temperatures of the late spring became apparent and this characteristic was followed up in considerable detail. Scudder mentions the effect

TABLE II

MAXIMUM FLY COUNTS AND TEMPERATURES AT INSIDE LOCATIONS

DATE	PERIOD OF MAXIMUM COUNTS	TEMPERATURE DURING PERIOD OF MAXIMUM COUNTS	MAXIMUM TEMPERATURE
Maximum above 30° C			
May 18	11–13	32.5	33
June 23	10–11	29	32
July 14	10	29.5	32
July 22	11	29.5	32
July 27	9–15	31.5	35
July 29	9–10	29.5	34
Aug. 16	10–11	28	33
Aug. 19	10	30	33
Aug. 21	10	29	32
Maximum at or below 30° C			
Feb. 20	9–10	19	20
Mar. 17	11–13	24	25
Apr. 12	9–16	25.3	26.5
May 19	12–14	29.4	30
Sept. 14	11–12	29.5	30
Sept. 15	11–15	28.6	29
Sept. 16	10	27.5	30
Sept. 28	10–13	28.5	29.5
Sept. 30	11	28.5	29.5
Oct. 21	14	26.8	28
Oct. 25	12–15	26	27
Oct. 26	16	27.5	28.5
Nov. 10	14–15	27.7	30
Nov. 30	11–13	18	20
Dec. 16	9–15	18.8	20

of extreme midday heat in dispersing flies from normal outdoor patterns. In Egypt this dispersal is probably even more marked. However, the fact that the doors and skylights are nearly always open and never screened permits the flies to choose inside or outside locations quite freely and made possible a study of relative concentrations both diurnally and annually.

In order to determine to what extent relative fly concentrations varied during the day, grill counts and temperatures were taken at

hourly intervals both inside and outside of houses. Five zones which previous data had shown to give the highest inside counts most consistently were chosen and grill counts were taken both inside and outside, beginning on the hour, from early morning to sunset. The average of these five counts is the hourly index. The index figures are necessarily relative and the counts are probably weighted in favor of inside concentrations, because zones were selected on the basis of inside high counts. This was done because, as discussed above, there is less variation in the consistency with which inside locations maintain their position among the highest zones.

TABLE III

MAXIMUM FLY COUNTS AND TEMPERATURES AT OUTSIDE LOCATIONS

DATE	PERIOD OF MAXIMUM COUNTS	TEMPERATURE DURING PERIOD OF MAXIMUM COUNTS °C	MAXIMUM TEMPERATURE °C
Feb. 20	13–15	23.3	24
Mar. 17	10–12	24.7	27
Apr. 12	9–10	23.3	29
May 18	7–8	26	36
May 19	8	26.5	35
June 23	7	24.5	35
July 14	6	27	32
July 27	7	28	38
July 29	7–9	28.3	38
Aug. 16	5–8	23.5	34.5
Aug. 19	6	25	34.5
Aug. 21	6	22.2	30.5
Sept. 14	7–11	24.3	33
Sept. 15	7–10	25	31
Sept. 16	10	29	33.5
Sept. 28	11	29	30.5
Sept. 30	11	26.7	30.5
Oct. 21	10–14	26.7	28.5
Oct. 25	7–12	24	29
Oct. 26	11	26	30
Nov. 10	12–15	28.3	32
Nov. 30	12–14	19.5	20
Dec. 16	12–14	21	22

The hourly counts were made on twenty-four days selected to represent all seasons but mostly from months when flies are numerous. Table II lists, for inside locations, the hours of the day during which the highest counts occurred, the average temperatures during that period and the maximum temperature reached for the day. The same information for outside locations is given in Table III.

The period of maximum counts was estimated from the hourly fly index curves. Twelve of these are shown in figures 3 and 4. Where obvious peaks occur the single hour and temperature is recorded as

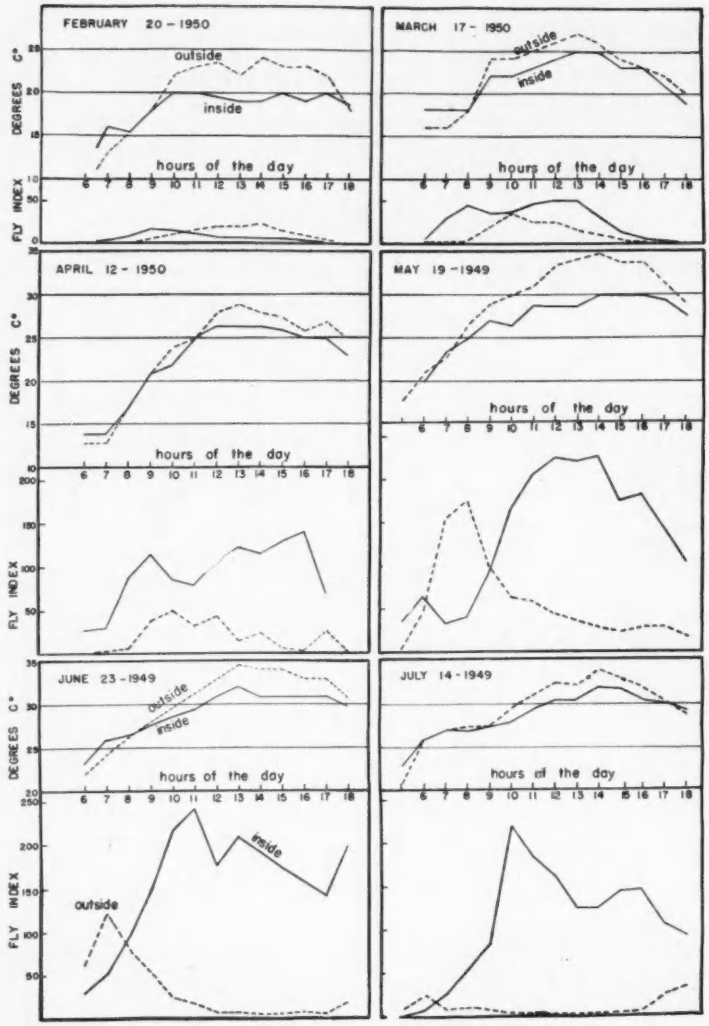


FIG. 3. Hourly temperatures and fly counts at Ashtar, February to July.

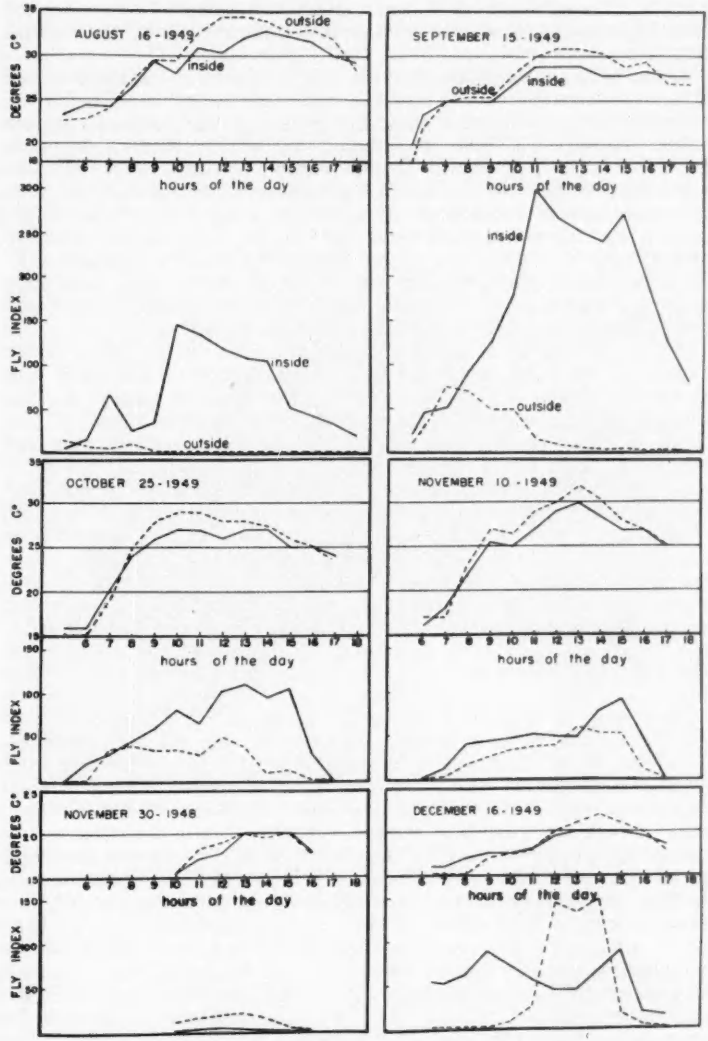


FIG. 4. Hourly temperatures and fly counts at Ashtar, August to December.

the time of highest count. Where there are high levels at several hours or throughout the day, the average temperature of the three or more high points was considered as the temperature of the highest counts.

On nine days from May through August the temperature at which inside maximum fly counts occurred was close to 30° C although the maximum temperatures for these days were generally several degrees higher (Table II). When maximum temperatures were at or below 30° C the highest fly counts on fifteen days occurred, with only two exceptions, within two degrees of the maximum temperature reached. At outside locations maximum fly counts on twenty days from March to early November occurred between 23° C and 29° C although maximum temperatures on these days ranged from 27° C to 38° C (Table III). On three days in February, November and December when maximum temperatures were below 26° C the highest fly counts were found within one degree of the maximum temperature reached.

These observations suggest certain principles as to the behavior of flies in terms of temperature. The indicated trends show how certain previously demonstrated principles may be applied to field problems. Dakshinamurty (1948) used temperatures of 35° C and 18° C to limit the flight grade of activity in his experiments and demonstrated that flies move towards 30° C in either a 30° C – 40° C or a 20° C – 30° C range. Either or both of these considerations may be involved in the occurrence of maximum inside counts in Egyptian villages at temperatures closer to 30° C and several degrees below the maximum temperatures reached. Flies might be moving to cooler parts of the house away from the attraction centers where the grill counts were taken or, as temperatures approached 35° C, an actual reduction in flight activity might have occurred. The choice of 30° C in a 20° C – 30° C range would explain the occurrence of highest counts near the maximum temperature when this maximum was 30° C or below.

Similarly, at outside locations it would be expected that below 30° C the highest counts would occur close to the maximum reached, and closer to 30° C at higher temperatures. On the three days when outside temperatures were 24° C and below, the temperature of highest counts was within one degree of the maximum, as expected. However, when outside temperatures were above 25° C the temperature for highest fly counts averaged 26° C instead of 30° C. This is seemingly inconsistent with both the laboratory findings of Dakshinamurty and the data for inside locations. A study of the daily graphs (figs. 3 and 4) shows that from April to September as temperatures rise from 20° C to 30° C, a falling outside curve is accompanied consistently by a sharply rising inside curve. In other words it would appear that as outside temperatures rise above the vicinity of 25° C flies tend to move inside in ever increasing numbers. The most probable explanation is the presence of more powerful attraction foci at inside locations. This should be generally true since zones were selected on the basis of high inside counts. Temperature may be the dominant factor in the lower portion of the 20° C – 30° C range but in the upper portion it would be expected that temperatures would be near enough to optimum so that

strong attraction foci could overcome the temperature factor and flies choose the inside locations.

Relative humidity does not appear to be a factor in this dispersal to the inside. Dakshinamurty (1948) found that a low relative humidity was favorable to fly activity at high temperatures but at lower temperatures differences in relative humidity did not show any marked differences in activity. Although dry air was preferred when temperatures were between 27° C and 33° C, at greater extremes temperature became the dominant factor. In Egypt high temperatures are rarely associated with high humidities so that excessive moisture is less likely to be a limiting factor to fly activity. Average inside

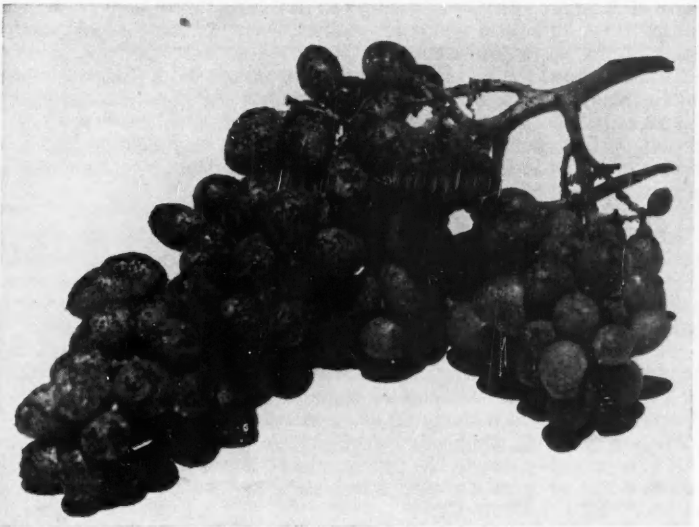


FIG. 5. Fly feces accumulated on a night resting place.

and outside relative humidities between 1000 and 1200 for the month of June, 1948, were 50% and 45% and for July, 1948, they were 62% and 59%. Even if flies could detect such small differences in relative humidity the drier air was consistently outside and therefore could not account for the dispersal to the inside.

The movement of flies to warmer locations at lower temperatures is evident in most of the daily graphs (figs. 3 and 4). This dispersal is indicated by the direction of the curves rather than index levels except where extreme differences occur. For example, on February 20th the inside curve rises while inside temperatures are higher but when outside conditions begin to become warmer the inside curve begins to decline and the outside curve to rise. A similar condition is found on March 17 until the outside curve starts a downward trend

as temperatures rise above 25° C and temperature probably becomes a less effective factor than inside attractions. The same behavior is found reflected in all the daily graphs with few exceptions.

A feature of the daily curves which does not appear to be related to temperature is the consistent fall of the grill index both inside and outside during late afternoon even when temperatures remain within the optimum range. This may be associated with approaching sunset inasmuch as the drop tends to occur later in summer than in winter months. Observations of night time resting places from May to October disclosed great numbers of flies clustered on tree leaves and other vegetation just outside the village houses (fig. 5). This gathering of flies has been found on several occasions as early as between one and two hours before sunset. Shaking the tree branches to disturb the flies caused them to swarm about for a short time but they quickly settled again on the leaves and remained there until at least 2200 and presumably throughout the night. In April after sunset more flies were noted on clothing, hanging objects and walls inside the houses than on tree leaves outside. Temperatures are usually lower than inside soon after sunset so that selection of night resting places may also be based on choice of cooler locations in hot weather and warmer locations when it is cold.

The above discussion may be summarized as follows:

1. When temperatures are below approximately 20° C flies tend to concentrate in warmer locations at any time of day and probably regardless of the strength of attraction foci. When temperatures rise more than two or three degrees above 30° C flies tend to concentrate in cooler locations at any time of day regardless of attraction foci.

2. When temperatures are between 20° C and 30° C there is a tendency for outside counts to rise with temperatures up to the vicinity of 25° C. Above 25° C the flies begin to move inside with a resultant drop of the outside counts and an accelerated rise of the inside counts. This movement to the inside before outside temperatures have reached 30° C is probably due to the presence of stronger attraction foci inside, which begin to exert a greater influence than temperature in the range between 25° C and 30° C.

3. The greater variation in the temperature at which maximum counts occur for outside locations and therefore of the associated time of day makes it preferable to use inside counts for routine checks on fly abundance. At Egyptian villages inside counts are generally highest between the hours of 1100 and 1300 during May, June and September, between 1000 and 1200 during July and August and between 1200 and 1500 during cooler months.

4. There is a marked tendency for the fly index to fall during late afternoon regardless of temperature conditions and this is probably due to approaching sunset and selection of night-resting places rather than temperature.

SEASONAL VARIATIONS

The relative fly abundance at bi-weekly intervals (based on counts on four days per week) is shown for two villages in figures 6 and 7. Inside counts were made at approximately the period of maximum

activity (from 1000 to 1200 during July and August and from 1100 to 1400 during the other months). The inside and outside temperatures at Ashtar taken at the time counts were made and the mean temperatures for 1948 and 1949 based on the Giza Province meteorological reports are also plotted for comparison (fig. 6).

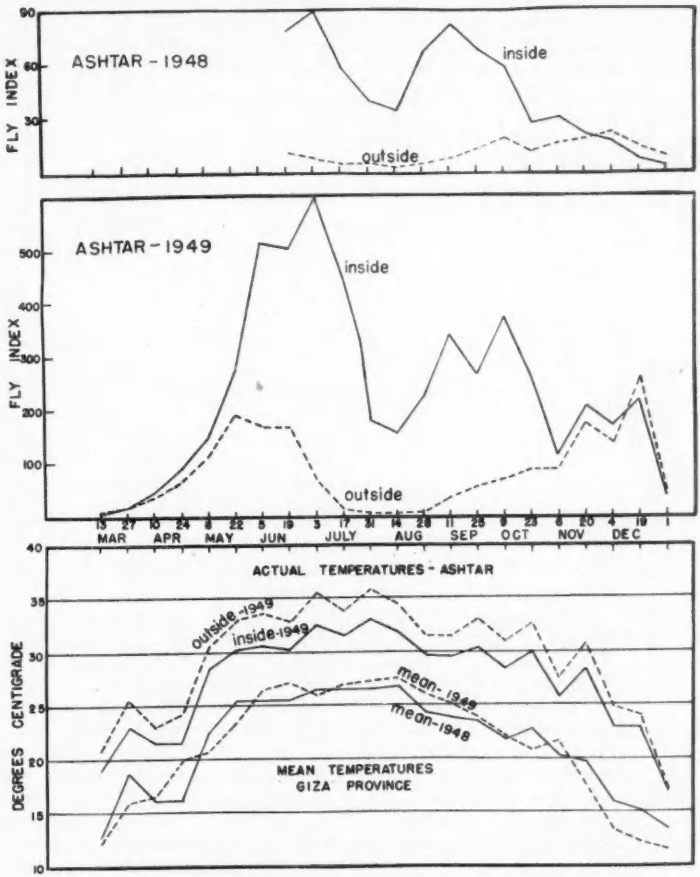


FIG. 6. Seasonal variations in fly abundance at Ashtar (1948–1949) compared with temperatures.

Consistent seasonal trends were found at all villages. The peaks and low points of fly abundance occur at approximately the same date at Ashtar in 1948–1949 (fig. 6). Even in the villages where insecticides were occasionally applied there is an obvious trend towards the occurrence of high and low indices at about the same time (fig. 7).

The most prominent feature of the seasonal curves is the occurrence of the annual peak of the inside fly index during the latter part of June and the very steep drop of the inside curve during July and August. A secondary inside peak was also found at all villages during September or early October followed by decreasing inside counts from October to December. Outside counts begin to drop in May several weeks before there is any marked reduction of inside counts and this is probably associated with the movement of flies to the inside. Outside counts during July and August are extremely low but again increase

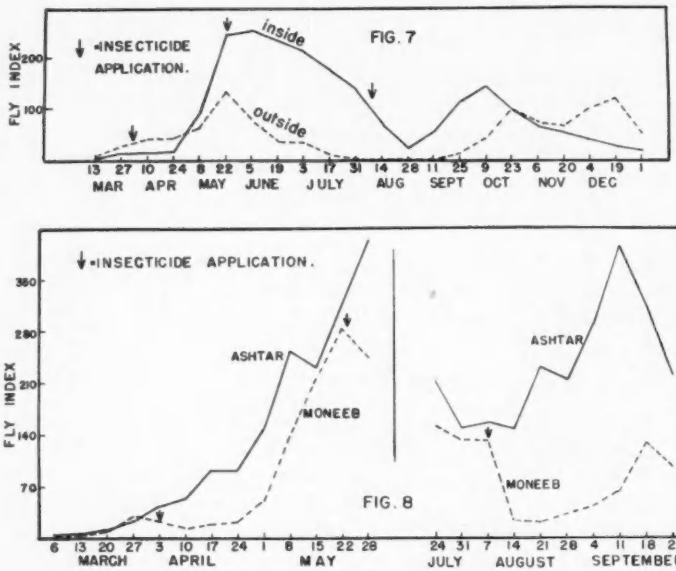


FIG. 7
INSECTICIDE APPLICATION.
inside
outside
FLY INDEX
200
100
13 27 10 24 8 22 5 19 3 17 31 14 28 11 25 9 23 6 20 4 19 1
MAR APR MAY JUNE JULY AUG SEPT OCT NOV DEC
INSECTICIDE APPLICATION.
ASHTAR
MONEEB
FLY INDEX
360
280
210
140
70
FIG. 8
6 13 20 27 3 10 17 24 1 8 15 22 28 24 31 7 14 21 28 4 11 18 25
MARCH APRIL MAY JULY AUGUST SEPTEMBER

FIG. 7. Seasonal variations in fly abundance at Moneeb, 1949.

FIG. 8. Reaction of fly grill index to single applications of insecticides to breeding areas at Moneeb.

during the fall. The last part of December shows an abrupt drop of all grill counts which continue to decline through January to the annual low point in February. Although many of the grill counts were zero and the index was too low to show at all on the scale used, there was never a day during February when at least a few flies could not be found. The average minimum temperature for February, 1949, was 4.9° C and the mean temperature was 11.3° C.

The annual cycle of housefly prevalence in Egypt follows a typical pattern which appears to be closely associated with the temperature cycle. From an extremely low density in winter flies increase rapidly throughout March, April and May as mean temperatures rise from 15° C to 25° C. During May flies tend to move more and more to the

inside of houses where temperatures during most of the day are close to 30° C, several degrees below outside temperatures. In June it is probable that the higher temperatures begin to affect fly abundance by causing a decrease in activity and breeding and possibly by increasing fly mortality. In any case, fly populations drop rapidly during July and most of August, both inside and outside as daily mean temperatures rise above 25° C. At the end of August actual temperatures inside begin to drop closer to 30° C and mean temperatures nearer 25° C. This is accompanied by an increase of fly densities inside of houses. Fly populations increase during September both inside and outside but more rapidly inside where temperatures are below 30° C. From October to December flies again move outside as temperatures fall from 30° C to below 25° C. The general level of fly densities from September to December never approaches the very high densities which occur during the spring. At the end of December mean temperatures are below 15° C and fly populations both inside and outside drop to a low winter level.

Lorincz and Makara (1936) present seasonal fly density curves for Hungary which follow the rise of five-day mean temperatures above 16° C until a summer high level is reached in July. This high level is maintained until October *without the extreme summer depression* such as is found in Egypt. The mean temperature curve which they give for the summer in Hungary is for the most part under 24° C and only once reached 25° C. During October the mean temperature dropped from 19° C to below 10° C and was accompanied by a precipitate fall of the fly density curve.

The fly grill indices shown by Scudder (1947) based on counts made in Texas and Georgia reveal extremely high June peaks and low points in July and August followed by secondary and smaller peaks in the fall. The obvious similarity of these graphs to the seasonal profile for Egypt is of considerable interest from the standpoint of insect chorology. A comparison of mean summer temperatures for Texas, Georgia and Egypt, which are all at approximately the same latitude, with those of Hungary, fifteen to twenty degrees further north, might be significant in connection with fly population variations.

CONTROL EVALUATION

Since the grill method provides only a relative index of fly densities it is more dependable for following weekly changes in the same village than for comparing actual densities from one village to another. Scudder (1947) has demonstrated, however, that it is nevertheless a useful tool for comparison of different establishments and areas inasmuch as the grill index is consistent with independent sanitary ratings. In other words, it may be considered as a means of recording objectively the status of fly abundance which in degree of accuracy is far better than a general description even if considerably short of a true population estimate.

The consistency with which the weekly grill index follows the seasonal increase of the fly population, for example, the rise from early spring to June and the subsequent sustained drop to a summer low point (fig. 2) is good evidence of its practical value. One man should be able

to obtain a satisfactory relative fly index for one village in not more than fifteen to twenty-five minutes using the following procedure.

1. One count is made at each grill placement.
2. A group of the five or six usually highest zones in the village are selected after a two-week survey to determine these maximum zones.
3. One count is then made in each of the five or six selected zones daily, on two or three days a week. The average of the three highest daily counts is the daily index.
4. Inside counts alone should be sufficient for routine control evaluation, provided counts are made during a period of maximum activity and normal seasonal fluctuations are taken into account.
5. Counts should be taken at the time of day when fly activity and prevalence about attraction foci is at a high level, near 30° C for inside locations and near 25° C for outside locations.

Insecticide applications were made at three villages to test the sensitivity of the grill index to light dosages and single treatments. Figure 7 shows how applications at Moneeb tend to cut short the seasonal peaks or accelerate the slope of a falling index curve. In figure 8 portions of the Moneeb curve are shown at weekly intervals compared with the curves for untreated Ashtar. A marked change in direction and slope is evident for several weeks after each treatment. Obviously the significance of these changes depends on how consistently treated and untreated units have maintained their relative positions before control is initiated. Fly count levels in 1948 during early summer, mid-summer and fall at Moneeb, Wali Bey and Harania were generally between 75% and over 100% of the Ashtar levels. During 1949, when occasional treatments were applied to these villages, the fly indices at the same dates varied from 20% to 45% of those of Ashtar. Even without a check village a grill index which remained at April levels throughout May and June would demonstrate highly effective control. The level of the grill index is also useful for determining when retreatments should be applied.

APPLICATIONS

The information accumulated on diurnal and seasonal dispersal of houseflies has considerable significance for both control operations and their evaluation. Airplane spraying, for example, if carried on while a high percentage of the fly population is concentrated within village houses could not be as effective as when the fly population is outside. The same would apply to aerosol dispersal equipment which did not direct the fog to the inside of houses. Conversely, the effectiveness of hand dispensers used inside would benefit from an inside fly concentration. Extreme differences in fly concentrations between inside and outside do occur, at least during the summer, so that this problem is of more than theoretical interest.

The importance of fly dispersal on the effectiveness of residual control methods is probably much less since flies seldom rest on outside walls. However, the possible value of placing toxic deposits on vegetation near village houses in order to take advantage of the night time resting habits of flies during warm weather is worth consideration.

Evaluation of control work could be quite misleading if based on

fly density estimations, by any method, which did not account for normal seasonal or local differences in abundance and dispersal. In the case of trapping methods, for example, the power of attractants could be influenced by the temperature range since beyond certain critical points temperature seems to become the more powerful factor. In applying the grill method several factors must be considered. Count zones must be selected to account for high fly concentrations or excessive time will be required to cover adequately an entire village. The variations of grill counts during the day are often so great that unless counts are made during the period of high fly activity the index may be of no value. The fly habit of concentrating at inside or outside locations according to certain temperature ranges must also be considered in regard to the type of information desired. Seasonal trends undoubtedly will vary at different latitudes. It is conceivable that in some areas a very low outside index in summer would not necessarily mean any decrease in total fly population but would indicate only that a major dispersal of the population to the inside had taken place.

These field observations in Egyptian villages, although dealing with a different subspecies, are quite consistent with the results of laboratory experiments on the reactions of *M. domestica* to temperature. It is probable that similar behavior, perhaps modified by different conditions of climate, house construction and breeding potentials, occurs in other parts of the world.

SUMMARY

Houseflies show a marked tendency to concentrate at the more attractive foci in Egyptian villages. Zones where fly concentration is greatest remain consistently among the highest count zones in the village, particularly for inside locations. This characteristic makes it possible to obtain a relative index of changes in fly abundance by making counts only at a few of the consistently high zones without time-consuming surveys of the entire village.

Housefly counts become progressively higher during the day as temperatures rise to approximately 30° C. As temperatures rise much above 30° C there is a tendency to decreased counts. There is usually a late afternoon drop in the fly index regardless of temperatures.

Houseflies tend to disperse between inside and outside of houses in Egyptian villages according to temperature differences. They consistently choose the inside or outside location corresponding with the higher temperature below 20° C and with the lower temperature above 30° C. It is probable that temperatures exert a greater influence on fly dispersal below 25° C and that attractions exert a greater influence between 25° C and 30° C. This dispersal of flies according to temperature differences may be useful for determining the best time for application of space sprays at outside locations, for example, airplane or ground fog applications. Likewise, space sprays applied inside would effect a greater kill when flies were concentrated inside.

Fly abundance in Egypt is at its low point during late December, January and February when mean temperatures are below 15° C. Flies increase rapidly in numbers from March to an extremely high annual peak in June. The rate of increase is greatest when mean

temperatures are between 20° C and 25° C. During July and August while mean temperatures are above 25° C fly abundance drops rapidly but rises again in September as temperatures go below 25° C. Throughout the fall fly densities increase but never to the extend found in May and June. As temperatures become lower from September to December flies tend to spend more and more of the day outside of houses.

Although the grill index method for comparison of fly densities does not provide a true population estimate it is sufficiently sensitive to provide useful information, when applied with due regard to fly dispersal, on the progress and effectiveness of control campaigns, especially where control work continues over a period of several weeks or months.

LITERATURE CITED

Dakshinamurty, S. 1948. The common housefly, *Musca domestica* L., and its behavior to temperature and humidity. Bull. Ent. Res., 39: 339–358.

Hafez, M. 1941. Investigations into the problem of fly control in Egypt. Bull. Soc. Fouad 1er Ent., 25: 99–144.

Hafez, M. 1941. A study of the biology of the Egyptian common housefly, *Musca vicina* Macq. Bull. Soc. Fouad 1er Ent., 25: 163–189.

Lorincz, F., and **Makara, G.** 1936. Investigations into the fly density in Hungary in the years 1934 and 1935. Quart. Bull. Hlth. Org. L. of N. 5, no. 2, pp. 219–227.

Scudder, H. I. 1947. A new technique for sampling the density of housefly populations. U. S. Pub. Hlth. Rep. 62, no. 19, pp. 681–686.

MANUAL OF ENTOMOLOGICAL TESTING METHODS

In 1948, the Entomology Subcommittee of the Chemical-Biological Coordination Center obtained information on insecticide testing from numerous laboratories and the results were distributed to participants. The Subcommittee planned to continue this successful survey.

Recently, after discussions with the American Association of Economic Entomologists and others, the Subcommittee believed that a book on testing methods in entomology would be more useful and, in April, 1951, Dr. Harold H. Shepard, U. S. Department of Agriculture, was designated editor.

The book will include toxicological and screening methods used by entomologists in this and other countries and will contain descriptions of methods detailed enough to permit them to be duplicated. It will be published by the National Research Council and sold at cost.

The Subcommittee will provide forms for those who wish to participate in this project by furnishing descriptions of the test methods which they use. Send request for forms to—

DR. RAIMON L. BEARD, Chairman,
Entomology Subcommittee,
Chemical-Biological Coordination Center,
National Research Council,
2101 Constitution Avenue,
Washington 25, D. C.

NOTES ON THE PHLEBOTOMUS OF PANAMA

(Diptera, Psychodidae)

VII. The Subgenus Shannonomyina Pratt[1]

G. B. FAIRCHILD and MARSHALL HERTIG
Gorgas Memorial Laboratory,
Panama, R. de P.

Subgenus **Shannonomyina** Pratt

Shannonomyina Pratt, 1947, Proc. Ent. Soc. Washington 49 (3): 86 (new name for *Shannonomyia* Dyar 1929).

Shannonomyia Dyar, 1929 (July), Amer. Jour. Hygiene, 10 (1): 117–118 (monotypic for *Phlebotomus panamensis* Shannon). Costa Lima, 1932, Mem. Inst. Oswaldo Cruz, 26 (1): 18 (no subgenera accepted). Mangabeira, 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 119 (6 species included). Mangabeira and Galindo, 1944, Amer. Jour. Hygiene, 40 (2): 190 (subgenus redefined). Not *Shannonomyia* Alexander, 1929 (January), Dipt. Patagonia S. Chile, 1: 142–143 (Tipulidae).

Psychodopygus Mangabeira, 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 237–238. (Type *Phlebotomus unisetosus* Mang., 1941).

This group has been variously treated. Accepted as a more or less valid subgenus by Mangabeira (1942), most other workers including Root (1934), Costa Lima (1932), Barretto (1947) and Floch and Abonnenc (1944) have admitted that the species form a group, but have refrained from using a name for it. Mangabeira and Galindo (1944) in their recharacterization of the group rely mostly on male characters, but as will be shown below, female characters appear to be more reliable for group separation. *Psychodopygus*, although striking enough in the male sex, has females very similar to typical *Shannonomyina*.

The group may be characterized as follows: *Phlebotomus* with palpal segments II and III long, subequal, IV very short, generally less than one-third of III, and V not more than twice as long as IV. Cibarium with four to eight horizontal teeth and usually with numerous erect teeth some of which are markedly enlarged. Pharynx unarmed. Abdomen usually covered with recumbent scale-like hairs. Spermathecae characteristic, consisting of six to ten or more deeply incised, imbricated rings and a more or less stalked terminal knob. Ducts of spermathecae long or short, arising from a common duct of variable length. Individual ducts, and usually part of common duct, characteristically wrinkled and sclerotized. Male genitalia without basal tuft on coxite, style with two to five spines, some of which may be reduced to fine setae. Lateral lobes usually as long as or longer than coxite, unarmed. Parameres simple to exceedingly complex, often

[1]This work was initiated under a contract recommended by the Committee on Medical Research, between the Office of Scientific Research and Development and the Gorgas Memorial Laboratory, and was done, in part, under a contract between the Army Medical Research and Development Board, Office of the Surgeon General, and Gorgas Memorial Laboratory.

Cost of publication is paid by the Gorgas Memorial Institute.

with one or more tufts of modified setae and long digitate processes. Aedeagus stout to slender, genital pump and filaments of the usual type for the genus.

Since the spermathecae are of the greatest importance in this group, we give here a somewhat extended discussion of their structure.

Terminal knob.—We use this descriptive but noncommittal term in the absence of any recognized nomenclature based on a study of the histology of the spermathecae. The knob and its radiating "hairs" are constant, conspicuous and often characteristic structures in most groups of *Phlebotomus*. We have observed in a number of species, particularly in freshly caught specimens cleared in phenol, an envelope surrounding the spermathecae and at times the ducts as well. This envelope may be entirely clear or irregularly refractive in whole or in part. In the case of ***paraensis*** (fig. 16), for example, most of the envelope is perfectly clear, but there is a sharply delimited refractive area surrounding the terminal knob. It is possible that this represents glandular tissue and that the hairs are actually ducts. In some groups there is no knob at all and the hairs form a patch on the distal end of the spermatheca.

Annulations of spermatheca.—The terminal annulation may be indented or deeply incised on one side. In ***panamensis*** this characteristically gives rise to marked asymmetry, with a terminal knob bent to one side (fig. 13).

The annulations of the spermathecae show a characteristic pattern of sclerotization which is particularly evident in well stained specimens. We have figured this only for ***paraensis*** (fig. 17) but it also occurs in all the other species of this group which we have seen. This pattern is on the inward-turned portion of each annulation and takes the form of a band with distal projections, recalling the colored glaze of some pottery.

Duct.—The transition between spermatheca and duct may be marked by one or two small but otherwise typical annulations. In reckoning the number of annulations the judgment of different observers will undoubtedly vary as to the inclusion of the smaller ones. It is therefore well to consider the recorded counts as implying "plus or minus one or even two." The smaller annulations may be followed by several small, irregular or abortive annulations, which in turn give way to a series of evaginated pouches which may characterize a considerable length of the duct. These pouches may be greatly compressed and lie at an angle with the duct axis, so that in optical section they give the impression of a "herringbone" pattern (*e.g.*, ***squamiventris***, fig. 21). These pouches greatly complicate the task of making drawings. The characteristic appearance under the microscope at times depends on a more or less regular pattern seen at the focal level of the duct axis, which it is relatively easy to represent in a drawing (*e.g.*, ***squamiventris***, fig. 21, ***paraensis***, fig. 18). In other instances the characteristic appearance is derived from the very confusion of successively superimposed images, with the lumen of the duct not obvious. In such cases we have elected to show in the drawings chiefly the outlines at the higher focal levels, *i.e.*, the external features of the duct (*e.g.*, ***geniculatus***, fig. 15). The evaginated pouches sooner or later give way to ridgelike thickenings on the outside of the duct lining, which may or may not form complete rings.

In all the species we have examined, those portions of the ducts with the imperfect annulations, pouches and thickenings, are sclerotized and conspicuous whether in phenol or in stained preparations. In many species the sclerotized portion ends rather abruptly, with the result that the rest of the duct is thin-walled and often very difficult to see, either in phenol or after staining. In *squamiventris* (fig. 21) this transition takes place on the individual ducts, which are relatively long, whereas in all or nearly all the other species, the sclerotized portion includes part of the common duct or may even extend to its base. Thus it is seen that in this group where the spermathecae are strikingly similar, the ducts are very important taxonomically.

For the sake of convenience, we append here an annotated check list of the species of *Shannonomyina*. Only original or especially pertinent references are cited. For fuller reference the reader is referred to Barretto's catalogue (1947). The biological data are mostly from papers by Barretto and colleagues working in Sao Paulo.

CHECK LIST OF THE SPECIES OF *Shannonomyina*

P. arthuri Fonseca 1936, Rev. Ent., 6: 324, figs. 1, 2, 6, 8 (♀; Sao Paulo, Brasil); 1939, Mem. Inst. Butantan, 12: 181–184, figs. 1–3 (♂; Sao Paulo, Brasil). The species has been reared from the egg, though only females were secured, so the association of the sexes is not certain, though very probable. It bites man and domestic animals avidly, both by night and by day in the forest. It is attracted to light and enters houses. So far known only from the State of Sao Paulo, Brasil, where it is locally common.

P. amazonensis Root 1934, Amer. Jour. Hygiene, 20: 244, figs. 1, 2, 3, (♀; Iquitos, Peru). Known with certainty only from the type material.

P. ayrozai Barretto and Coutinho 1940, An. Fac. Med. Univ. S. Paulo, 16 (1): 131–134, plate I, fig. 2, plate II, figs. 6–10 (♂, Sao Paulo, Brasil); 1943, Rev. Brazil. Biol., 3 (2): 183–185, figs. 1–4 (♀; Sao Paulo, Brasil). Male and female taken in copula. Collected at light in several places in the State of Sao Paulo, Brasil.

P. bispinosus n. sp. (See this paper for description and discussion.)

P. carrerai Barretto 1946, An. Fac. Med. Univ. S. Paulo, 22: 286–291, figs. 8–16 (♂, ♀; Restrepo, Colombia). Taken in copula. Known only from the types.

P. chagasi Costa Lima 1941, Acta Medica, Rio, 7 (1): 6, 8, 11, 13–14, figs. 1, 3 and in key (♀; Rio Negro, Amazonas, Brasil). Known only from the inadequately described type.

P. colas-belcouri Floch and Chassignet 1947, Inst. Pasteur Guyane, pub. 152, pp. 1–3 and fig. (♂; French Guiana). Known only from the type.

P. complexus Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36: 242–245, fig. 3 and plate 2 (♂; Piratuba, Para, Brasil). Known only from the type.

P. davisi Root 1934, Amer. Jour. Hygiene, 20: 242–244, figs. 1, 2, 3, 5 (♂, Fordlandia, Para; ♀, Caravellas, Bahia, Brasil). Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 249 (♂, ♀, Belem, Para, Brasil). Floch and Abonnenc 1944, Inst. Pasteur Guyane, pub. 90, pp. 11–12, fig. 8 (♂; French Guiana). This species has been taken in a number of other localities in Amazonas and Para. The Bahia females discussed by Root as well as females from Sao Paulo reported by others may or may not be properly associated.

P. geniculatus Mangabeira. (See this paper for full discussion.)

P. guyanensis Floch and Abonnenc 1941, Inst. Pasteur Guyane, pub. 15, pp. 17–20, fig. 6 (♀; French Guiana); *ibid.*, pub. 88, pp. 1–3, figs. 1–2 (♀; French Guiana). Known only from two female specimens from French Guiana.

P. hirsutus Mangabeira 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 116–119, figs. 8–13 (♂, Para, Brasil). Known only from the type.

P. lloydi Antunes 1937, Rev. Biol. Hig., 8: 24 (♀; Sao Paulo, Brasil). Coutinho, 1940, Arq. Zool. Est. S. Paulo, 1 (8): 331–333, figs. 1–3 (♂; Sao Paulo, Brasil). Barretto 1943, Observacoes sobre a biologia, em condicoes naturais, dos

flebotomos do estado de Sao Paulo; Thesis, Univ. Sao Paulo, pp. 119–120. The species has been taken in fair numbers only in a few localities in southeastern Sao Paulo. It enters houses occasionally, apparently attracted by light, but shows little inclination to bite man or laboratory animals and cannot be induced to feed on cold-blooded vertebrates. Rearing from eggs laid by captive females has not been successful, nor have matings been observed between the supposed sexes in captivity.

P. maripaensis Floch and Abonnenc 1946, Inst. Pasteur Guyane, pub. 140, pp. 1–3, fig. 1 (♂, French Guiana). Known only from the type taken in the forest near the Brasilian border.

P. panamensis Shannon. (See this paper for full discussion.)

P. paraensis Costa Lima. (See this paper for full discussion.)

P. rooti Mangabeira 1942, Mem. Inst. Oswaldo Cruz, 37 (2): 112–115, figs. 1–7 (♂; Para, Brasil). Doubtfully distinct from *davisi* Root, as Mangabeira himself admits. Known only from the types.

P. squamiventris Lutz and Neiva. (See this paper for full discussion.)

P. unisetosus Mangabeira 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 238–242, figs. 1, 2 and plate 1 (♂, Para, Brasil). Known only from the unique type.

P. sp. no. 780 Floch and Chassignet 1948, Inst. Pasteur Guyane, pub. 170, pp. 1–2, fig. 1 (♀; French Guiana). This unnamed species is closest to *guyanensis* F. & A. and *bispinosus* n. sp. It differs from the first in much shorter individual ducts of the spermathecae and from the last in the much longer common duct. It differs from nearly all other described females in having the common duct completely sclerotized. It is quite likely the female of some known male, as the authors stated when they refrained from naming it.

As can be seen by the above list, the majority of the species are known only in a single sex, and there is some doubt as to the association of the sexes in some of those known in both sexes. Enough is known, however, to show that females with very similar spermathecae, palpi and cibaria may be associated with males of widely different genital structure. Grouping of the males on number of spines on the style or structure of the parameres does not yield groups homogeneous for other characters and is useful only for key purposes. The inclusion of *Psychodopygus* here rests on the finding (in Colombia) of the male of *squamiventris* L. and N., which turns out to be a species very close to *complexus* Mang., and of both sexes of *geniculatus* Mang. in Panama. It is probable also that *maripaenis* F. and A. will turn out to be the male of *guyanensis* F. and A. or of "Species no. 780" of Floch and Chassignet.

There are a number of names in this group which appear to us of doubtful utility, but lacking adequate material we hesitate to discard them. It is possible that some may prove useful in a subspecific sense. Thus the differences between *hirsutus* Mang. and *colas-belcouri* Floch and Chass. consist in a slight difference in the position of the basal spine of the style while between *rooti* Mang. and *davisi* Root a slight difference in the relative lengths of the two arms of the paramere seems the only character separating the species. *Ayrozai* B. and C., *paraensis* C. L. and *carrerai* Barr. show a progressive development of the setae and arm of the paramere apparently correlated with geographical factors, but the females of *ayrozai* and *carrerai* are known with certainty, having been taken in copula, and are easily separated by the length of the individual ducts of the spermathecae. The female of *paraensis*, hitherto unknown, is described below.

We give below keys to males and females of the species here placed in *Shannonomyina*. We have studied material of both sexes of *panamensis, squamiventris, paraensis, geniculatus*, and *bispinosus* n. sp.

The other species are placed in the key on the basis of published descriptions, which in some cases have been inadequate. Thus we do not find adequate descriptions of the female cibaria of *chagasi*, *lloydi*, and *arthuri*. The first we have keyed out with *squamiventris*, as the original description seems to us inadequate. Costa Lima separates these two species on palpal measurements. The condition of the erect teeth in the cibaria of *lloydi* and *arthuri* seems not to have been described, so we have assumed they are as in *panamensis*. Should this be an error, they will key out with *amazonensis*, being easily separated by the number of horizontal teeth.

Males and females of the following species have been taken in copula or reared from eggs laid by known females: *carrerai*, *lloydi* and *ayrozai*. A single male of *squamiventris* was taken in an animal-baited mosquito trap with 50 females. No other species were present. Males of *panamensis* have been taken in Panama resting on humans in company with the biting females, in animal-baited mosquito traps as well as light traps, and there is little doubt as to the association of the sexes on morphological grounds as well. We have taken *geniculatus* males and females at light in a Shannon trap on a single occasion and in the absence of other species of this group, while both sexes of *paraensis*, were similarly secured. In the case of *davisi*, there is room for doubt as to the proper association of the sexes, as the male was from Para, while the female came from Bahia.

KEY TO MALES

1. Parameres simple. Style with two or four spines 2
   Parameres with modified setae or digitate processes, or style otherwise 4
2. Style with two terminal spines ..... **bispinosus**
   Style with four spines 3
3. Spines of style grouped closely near the end of the style, which is nearly as long as the coxite ..... **arthuri**
   Spines distributed as follows: two terminal, one subterminal, one near the middle of the style. Style short, hardly half length of the coxite .... **lloydi**
4. Style with a single curved terminal spine and three slender subterminal setae 5
   Style with at least three strong spines. Parameres with strong modified setae and a digitate process 9
5. Parameres slender, ending in a slender upturned digitate process, without strongly modified setae or hair tufts. Coxite normal, about as long as style. Lateral lobes shorter than coxite ..... **geniculatus**
   Parameres stout, highly modified. Coxite inflated, constricted in middle ... 6
6. Parameres with a large tuft of long and numerous erect setae on a short, stout upturned arm and with a membranous foliaceous process at its apex ..... **unisetosus**
   Parameres otherwise 7
7. Parameres terminating in a long slender arm bent downwards at right angles to the basal part of the parameres and ending in a thin blade-like expansion ..... **maripaensis**
   Parameres otherwise 8
8. Parameres with a terminal, slender curved arm bearing a single delicate blade-like spine near its tip[2] ..... **complexus**
   Parameres as above, but the arm bearing two spines[2] ..... **squamiventris**
9. Style with five well developed spines. Parameres deeply biramous, the upper arm bearing heavy blade-like spines on its ventral surface 10
   Style with three well developed spines and a fine seta, which is sometimes spine-like, but always markedly slenderer than the other spines 11

[2]These structures are difficult to describe and differentiation must be left to the accompanying figures.

10. Lower arm of paramere markedly longer than spine-bearing arm.....**rooti**[3]
Lower arm of paramere about equal to spine-bearing arm.....**davisi**[3]
11. Parameres with two distinct tufts of blade-like setae on the upper surface and a terminal upturned arm bearing two long setae at its tip. Style with seta rather heavy, but more slender than other spines.....**panamensis**
Parameres with but a single tuft of setae. Seta of style very fine.....12
12. Setae of paramere long, numerous and blade-like. Arm long and slender, arising quite far towards the base of the paramere.....**hirsutus**
.....**colas-belcouri**
Setae of paramere not blade-like, less densely set. Arm arising at or near the apex of the paramere.....13
13. Setae short, about 20 in number. Arm short, arising nearly terminally.**ayrozai**
Setae longer, about 30 in number. Arm longer and arising further from the apex.....**paraensis**
Setae much longer, about 60, their area of implantation greater. Arm long, arising nearly terminally.....**carrerai**

KEY TO FEMALES

1. Individual ducts of spermathecae longer than the bodies of the spermathecae. 2
Individual ducts shorter than spermathecae..... 5
2. Common duct of spermathecae much shorter than the individual ducts. Spermatheca with 8 annulations.....**squamiventris**
.....**chagasi**
Common duct longer than individual ducts..... 3
3. Individual ducts more than twice as long as spermathecae. Common duct very long, three to four times individual ducts and completely annulated. Spermatheca with 8 annulations.....**guyanensis**
Individual ducts less than twice as long as spermathecae. Common duct shorter, its distal part tenuous and but faintly annulated. Spermatheca with 6 annulations..... 4
4. Palpal segments IV and V together about two-thirds as long as III..**geniculatus**
Palpal segments IV and V together only slightly less than III.....**ayrozai**
5. Erect teeth in cibarium subequal in size, the median ones not enlarged; four horizontal teeth. Spermathecae with about nine rings...**amazonensis**
A double row of markedly enlarged erect teeth in the cibarium..... 6
6. Terminal annulation of spermatheca markedly asymmetrical..... 7
Terminal annulation of spermatheca symmetrical or nearly so..... 8
7. Cibarium with six horizontal teeth.....**lloydi**
Cibarium with four horizontal teeth. Abdomen with scales dorsally. Mesonotum strongly infuscated. Palpal segments IV and V together about two-thirds as long as III.....**panamensis**
8. Cibarium with eight horizontal teeth. Palpal segments IV and V together nearly equalling III.....**arthuri**
Cibarium with four horizontal teeth..... 9
9. Common duct of spermathecae well sclerotized throughout, with clearly visible annular thickenings. Spermathecae with 7 to 8 annulations.....10
Common duct of the spermathecae well sclerotized for only a short distance below the junction of the individual ducts, the rest membranous, poorly sclerotized and visible with difficulty even in stained preparations. Spermathecae with 9 to 13 annulations.....11
10. Common duct much thicker than individual ducts, about 3.5 times as long as the individual ducts.....**bispinosus**
Common duct hardly thicker than individual ducts, about 5.5 to 6 times as long as the individual ducts.....Sp. No. 780
11. Palpal segments IV and V together equalling III. Mesonotum but slightly darker than pleura.....**carrerai**
Palpal segments IV and V less than III.....12
12. Abdomen without flat scale-like setae. Mesonotum hardly darker than pleura. Palpal segments IV and V together about five-eighths as long as III.....**paraensis**
Abdomen with numerous flat scale-like setae. Mesonotum somewhat infuscated. Palpal segments IV and V together about five-sixths as long as III.....**davisi**

[3]These two species doubtfully distinct. No material seen.

Phlebotomus (Shannonomyina) panamensis Shannon

Figs. 1, 2, 13, 26, 27, 34, 35, 40, 51

1926, Jour. Washington Acad. Sci., 16 (7): 192–193, fig. 1 (♂, ♀; Cano Saddle, near Gatun, Canal Zone, and other localities in Panama and the Canal Zone). Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22: 279–282, 2 figs; 1947, Arq. Zool. Est. S. Paulo, 5 (4): 216–217 (complete references). Fairchild, 1949, An. Rep. Gorgas Mem. Lab., 1948, p. 12.

A medium sized sandfly with markedly infuscated mesonotum and the abdomen clothed with flat white recumbent scales. The male genitalia have not previously been adequately figured, the original sketch of Shannon being quite misleading. Stone's sketch in Barretto (1946) shows the proportions, but is admittedly diagrammatic and does not indicate the broad blade-like character of the setae on the parameres. Ascoids simple, not quite reaching the ends of their respective segments, paired on all segments, but absent from the terminal three segments in the female, the terminal six in the male. Terminal three segments in both sexes noticeably shortened, pear-shaped. Newstead's scales scattered sparsely over the distal two-thirds of palpal segment III. Eyes rather large in both sexes. Palpi as figured, those of the male about one-third shorter than the female. Stem of genital fork rather slender and pointed in dorsal view. Gonapophyses of the eighth sternite (Sinton, 1925) short and slender. Spermathecae as figured, the common duct mostly very thin-walled and difficult to see. Annulations of spermathecae variable in number, 10 to 11 in our material, though others show up to 13, the terminal annulation markedly asymmetrical. Cerci rather slender. Cibarium as figured. Pharynx fairly broad and well sclerotized, its posterior end provided with numerous fine transverse wrinkles, apparently beset with minute spinules. Venation as figured, the veins and margin bearing numerous fine long hairs but no scales, though the hairs at the extreme base of the costa are somewhat lŏrate.

This species is one of the more abundant biting species in Panama, where it attacks both man and domestic animals. We have examined 1075 specimens, of which 19 were males. The great majority of these specimens were taken in horse-baited stable traps, 744 specimens including 3 males; 256 specimens were taken at light, either light traps of the automatic type with fan, or in Shannon traps using a gasoline lantern; 11 of these were males. Sixty-four specimens have been taken biting man, all, with the exception of 5 from the Rio Bayano area which were perhaps taken indoors, secured in the forest. A lot of several species, including a male and female of *panamensis*, were secured in a pigsty and biting pigs; a single female was taken in the ruins of Old Panama; and a lot of 6 males and 2 females were taken in buttresses near Almirante.

From the foregoing it is evident that we know little or nothing of the normal haunts or diurnal resting places of the species. In spite of many hundreds of searches of the usual type of daytime resting places in areas where the females were quite abundant, either biting man in the forest or attracted to lights or animal-baited traps, we have only twice taken the species in such habitats. In the forest it bites readily during the daytime as well as at night. During the course

of recent studies of forest mosquitoes by our colleagues quite a number of *Phlebotomus* have been taken both at ground level and at platforms in the tree tops. *Panamensis* has been quite often taken, but only at ground level. Although we have done little serious collecting in houses, we have records of *Phlebotomus* biting in houses a number of times, but these have all proved to be *gomezi* Nitz. The specimens mentioned above from the Rio Bayano were collected by Dr. H. W. Kumm in 1942 and may have been taken indoors.

The species seems quite widely distributed in Panama, probably more widely than our records indicate, as collecting with light or animal bait has been limited to a relatively few localities. We have specimens from Bocas del Toro, Chiriqui, Colon and Panama Provinces, though the bulk of our material is from animal-baited traps in the Canal Zone and vicinity. We have taken the species in every month save March and April, though our records show a preponderance of specimens in July and August. It is probably a rainy season species.

The literature records the species from Panama, Venezuela, Colombia and Peru, but so far as we are aware, males have been taken only in Panama. Records based on the female alone are open to question due to the difficulty of separating the various species of this group in that sex. In addition, we have seen females of what we believe to be *panamensis* from Mexico and Venezuela.

Phlebotomus (Shannonomyina) paraensis Costa Lima

Figs. 8–10, 16–19, 30, 31, 37, 41, 42, 52

1941, Acta Medica, Rio de Janeiro, 7 (1): 7, plate 1, figs. 1–3, and text fig. 2 (♂; Aura, Belem, Para, Brasil; taken in a Shannon trap). Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22: 282–286, figs. 3–7 (♂, Piratuba, Abaete, Para, Brasil). Abonnenc, 1948, Inst. Pasteur Guyane, pub. 177, p. 1–3, fig. 2, A, B (type seen and figured).

Phlebotomus ayrozai, Barretto and Pessoa, 1946, Livro homenagem a R. F. d'Almeida, p. 79 (in part). Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 188 (in part).

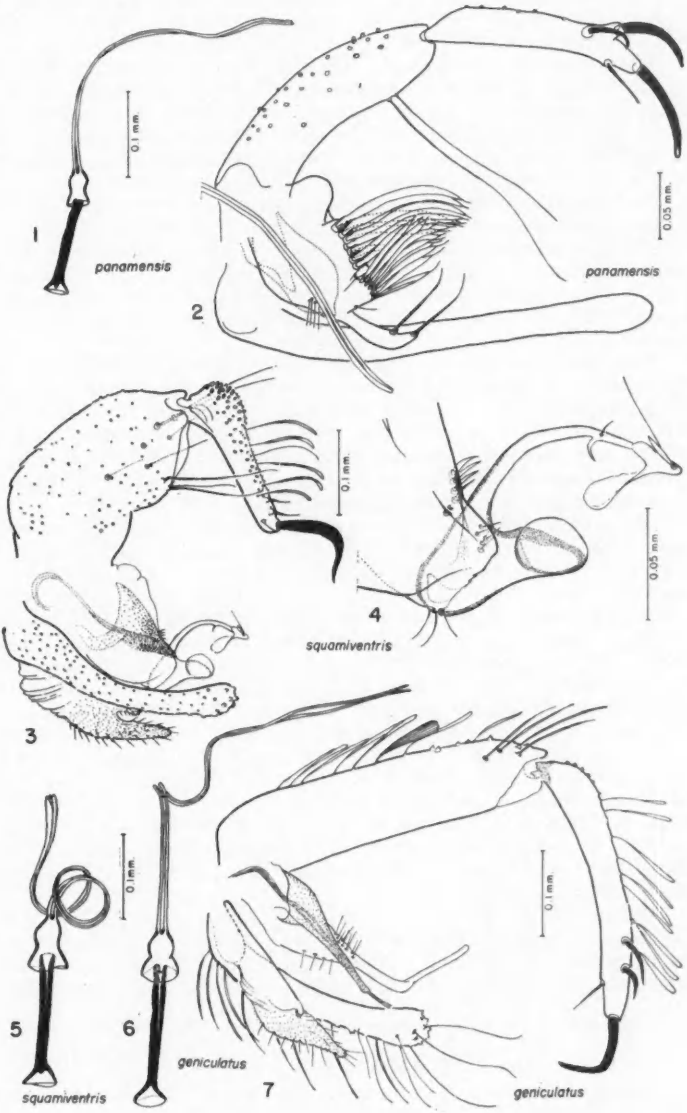
A medium sized pale colored sandfly with rather large eyes. Abdominal hairs recumbent or semi-erect, not scale-like. Wing venation as figured, the veins and margins clothed with long hairs, with a few lorate or ligulate scales at base of costa. Palpi as figured, shorter in the male, and with the terminal segments relatively longer in this sex. Ascoids simple, slender, long, but not reaching the ends of their

---

EXPLANATION OF PLATE I

FIG. 1. *P. panamensis*, pump and genital filaments. FIG. 2. Same, male genitalia, inner aspect; the two long hairs on the coxite are apparently the same as the deciduous hairs on the outer surface, but one or two commonly persist in this position in our series of specimens. FIG. 3. *P. squamiventris*, male genitalia, outer aspect. FIG. 4. Same specimen, paramere. FIG. 5. Same species, pump and filaments. FIG. 6. *P. geniculatus*, pump and filaments. FIG. 7. Same, male genitalia, inner aspect.

All drawings in this and subsequent plates were made by the authors with the aid of the camera lucida from stained copal-balsam preparations, except as noted. Magnifications are indicated on the drawings. With the exception of the male genitalia, each series of the same structure was drawn at the same magnification.


0.1 mm
1
panamensis
0.05 mm
2
panamensis
0.1 mm
3
0.05 mm
4
squamiventris
0.1 mm
5
squamiventris
0.1 mm
6
geniculatus
0.1 mm
7
geniculatus

respective segments; absent from the terminal three segments in the female, the terminal six in the male. Newstead's scales scattered sparsely over the distal two-thirds of palpal segment III.

Male genitalia as figured. Genital filaments slender, without modified tips, a little over three times as long as the pump. Female cibarium as figured. Pharynx broad, moderately sclerotized, with short, fine, digitate transverse ridges at its posterior end. Spermathecae as figured. Stem of genital fork long, slender and blunt. Gonapophyses of eighth sternite slender with a flaring membranous tip.

Our material differs in one respect from the descriptions of the two known specimens, both from Para, Brazil. Our specimens are uniformly pale yellowish, while both Para specimens are stated to have the mesonotum strongly infuscated. The position of the seta on the style varies somewhat, our figure showing a specimen with the seta placed quite far distally. Other specimens agree with the figures of Barretto and Costa Lima in this respect.

The females which we have associated with this species agree with the males in pigmentation, in lacking scales on the abdomen, and in wing measurements. Females were taken in numbers for some time before males were secured, our attention being attracted by their wholly pale color in contrast to the dark mesonotum of *panamensis*. Later both sexes were taken in Shannon light traps at a locality where the females had been taken abundantly biting man.

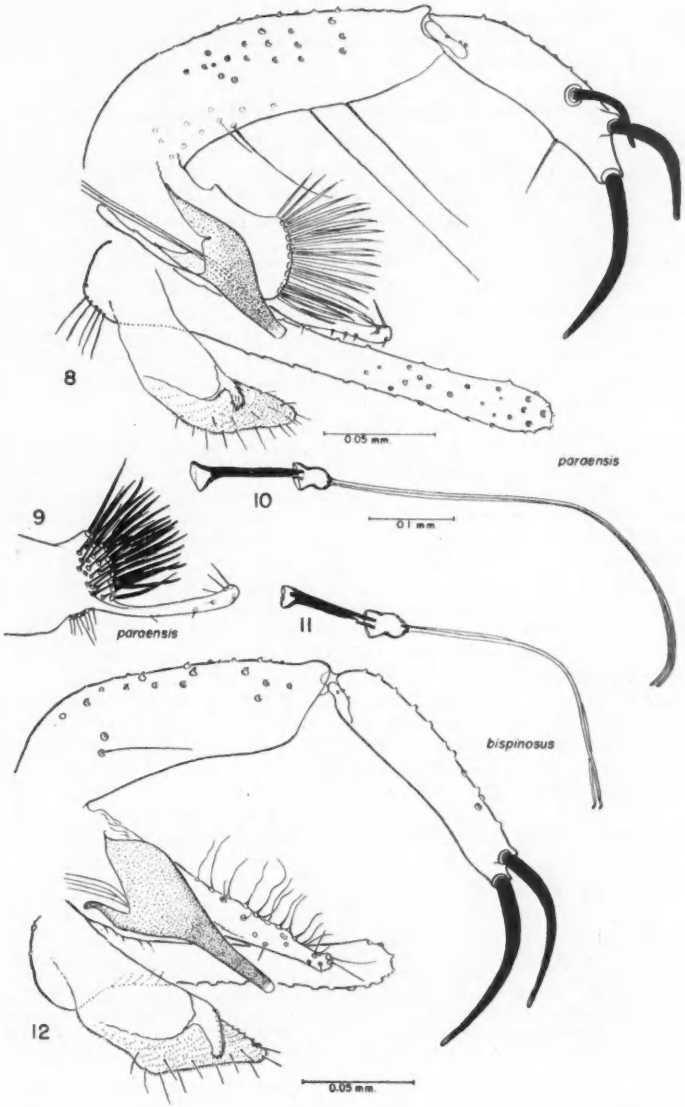
We have examined a total of 5 males and 129 females. Four males were taken in a light trap with 2 females, the other male was taken resting on a man, accompanying biting females. A single female was recovered from a lot of miscellaneous sandflies taken in buttresses, animal burrows and rock crevices. The remaining 126 females were all taken biting man in the forest during the daytime and at ground level. All the males and 102 of the females were taken at a single locality, Yellow Fever Station F, located in heavy forest at 1900 ft. elevation on the slopes of Cerro Campana, Panama Province. The remaining specimens were from the following localities in Panama: 2 ♀, Juan Mina, C. Z., 2 Sept., 1949; 1 ♀, 28 Oct., 1949; 1 ♀ Cacique, Colon Prov., 19 Sept., 1949; 1 ♀, upper Rio Pequeni, Panama Prov., 26 March, 1949, in buttresses or other crevices; 1 ♀, Yellow Fever Station X, Chorcha, Chiriqui Prov., 19 June, 1950, and 6 ♀, 19 Jan., 1951; 3 ♀, Yellow Fever Station A, Arraijan, Panama Prov., 5 June, 1950; 18 ♀ Candelaria Hydrographic Station, Rio Pequeni, Panama Prov., 14–23 August, 1950.

The majority of our specimens were taken in August with fair numbers in June and July, a few in September, one in October, 6 in January and one in March. This would indicate an early rainy season form, but too few light trap and biting collections have been made at

---

EXPLANATION OF PLATE II

FIG. 8. *P. paraensis*, male genitalia, inner aspect. FIG. 9. Same species, paramere of another specimen, outer aspect. FIG. 10. Same, pump and filaments. FIG. 11. *P. bispinosus*, pump and filaments. FIG. 12. Same, male genitalia, holotype.


8
0.05 mm.
paraensis
10
0.1 mm.
9
paraensis
11
bispinosus
12
0.05 mm.

suitable localities at other seasons for any definite statements to be made. The information available to date on this species indicates habits very similar to those of *panamensis*, but with more restricted habitat preferences.

Phlebotomus (Shannonomyina) bispinosus sp. nov.

Figs. 11, 12, 14, 28, 29, 36, 43, 46, 50

A medium sized sandfly with the mesonotum moderately infuscated and the eyes of average size. Abdomen with the tergites clothed with broad flat striate scales and with longer simple setae on the lateral and posterior margins. Sternites with only long semi-recumbent hairs. Second sternite as figured. Wings with venation as figured, clothed with long slender hairs, except at the base, where there are numerous large striate scales. Palpi as figured, those of the male a little more than half as long as those of the female. Newstead's scales sparse and long, scattered over the distal three-fourths of segment III. Ascoids as figured, absent from the terminal three segments in the female, the terminal six in the male.

Male genitalia as figured. Pump with expansion of plunger rather small (the "pavillon" of Parrot). Genital filaments rather stout, the distal fourth minutely annulate, tips simple, about twice as long as pump. Female cibarium as figured. Pharynx with numerous transverse minutely spinulose ridges at posterior end. Spermathecae as figured. Stem of genital fork broad and bladelike. Gonapophyses of eighth sternite slender and pointed.

Holotype male, slide 2344, La Victoria, Cerro Jefe, Panama, 29 Aug., 1950. Taken at light in a Shannon trap at Yellow Fever Station C, 1200 ft. elevation, in heavy forest. M. Hertig and P. Galindo colls.

Allotype female, slide 2359, same data as holotype.

Paratypes, 9 males, slides 2342–2343 and 2345–2351 and 9 females, slides 2352–2358 and 2360–2361, same data as holotype; 1 female, slide 2055, Juan Mina, Canal Zone, 20 Dec., 1949, in fan-type light trap, H. Trapido coll.; 3 females, slides 2383, 2386–2387, same data as holotype, but taken biting the collectors; 49 males, 33 females in alcohol, same data as holotype.

This species seems most closely related to *arthuri* Fons. in the male sex, having simple parameres and the spines of the style both nearly

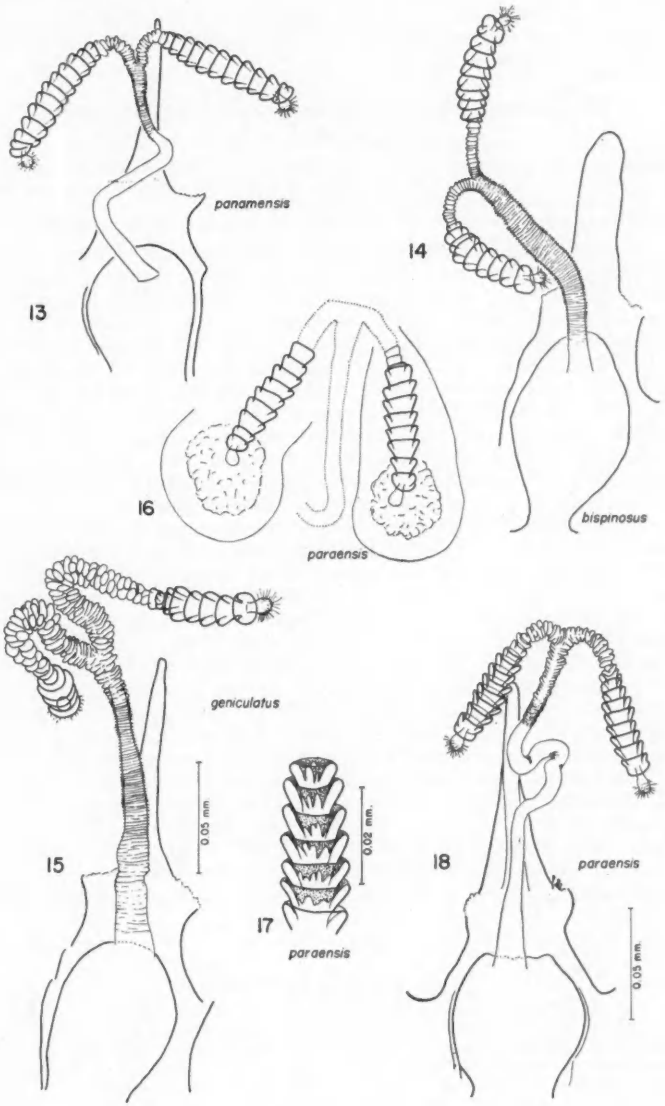
---

EXPLANATION OF PLATE III

As will be noted from this plate and from figs. 21–23 of the next plate, the spermathecae of this group are strikingly similar, but the ducts show a number of distinct characteristics which are important taxonomically.

FIGS. 13, 14, 15, 18, spermathecae, ducts and genital fork, dorsal aspect, all at the same magnification. FIG. 13. *P. panamensis;* note asymmetrical terminal annulation, terminal knob bent to one side. FIG. 14. *P. bispinosus;* note very broad stem of genital fork. FIG. 15. *P. geniculatus*. FIG. 18. *P. paraensis*.

FIG. 16. *P. paraensis*, freshly killed specimen in phenol; clear envelope surrounding spermathecae, with refractive area (glandular tissue?) surrounding terminal knob. FIG. 17. Same, detail of spermatheca, showing pattern of sclerotization, found also in the four other species figured in this paper.


panamensis
13
14
bispinosus
16
paraensis
geniculatus
15
0.05 mm
0.02 mm.
17
paraensis
18
paraensis
0.05 mm

terminal. In the female it most resembles the unnamed "Species no. 780" of Floch and Chassignet, differing in the shorter and thicker common duct of the spermathecae and in the spines of the cibarium not being laterally placed.

Phlebotomus (Shannonomyina) geniculatus Mangabeira

Figs. 6, 7, 15, 20, 32, 33, 38, 44, 47, 48

Phlebotomus (Psychodopygus) geniculatus Mangabeira, 1941, Mem. Inst. Oswaldo Cruz, 36 (3): 245–249 (♂; Belem, Para, Brasil, in horse-baited Shannon trap). Fairchild, 1943, Amer. Jour. Trop. Med., 23 (6): 571.
Phlebotomus geniculatus Barretto, 1947, Arq. Zool. Est. S. Paulo, 5 (4): 202.

A medium sized sandfly with the mesonotum and abdominal tergites quite strongly infuscated. Eyes of average size for the genus. Tergites mostly clothed with semi-recumbent setae, a few of which, especially on the second and ninth tergites, are lorate or strap-shaped. Sternites with only long semi-recumbent hairs. Wings with venation as figured, clothed with long slender hairs except at the base, where there are numerous large striate scales. Palpi as figured, those of the male about one-fourth shorter than those of the female. Newstead's scales sparsely scattered over the distal three-fourths of palpal segment III. Ascoids as figured, absent from the terminal three segments in the female, the terminal six in the male. Second sternite as figured. Cerci of male quite acutely pointed, of female much less so.

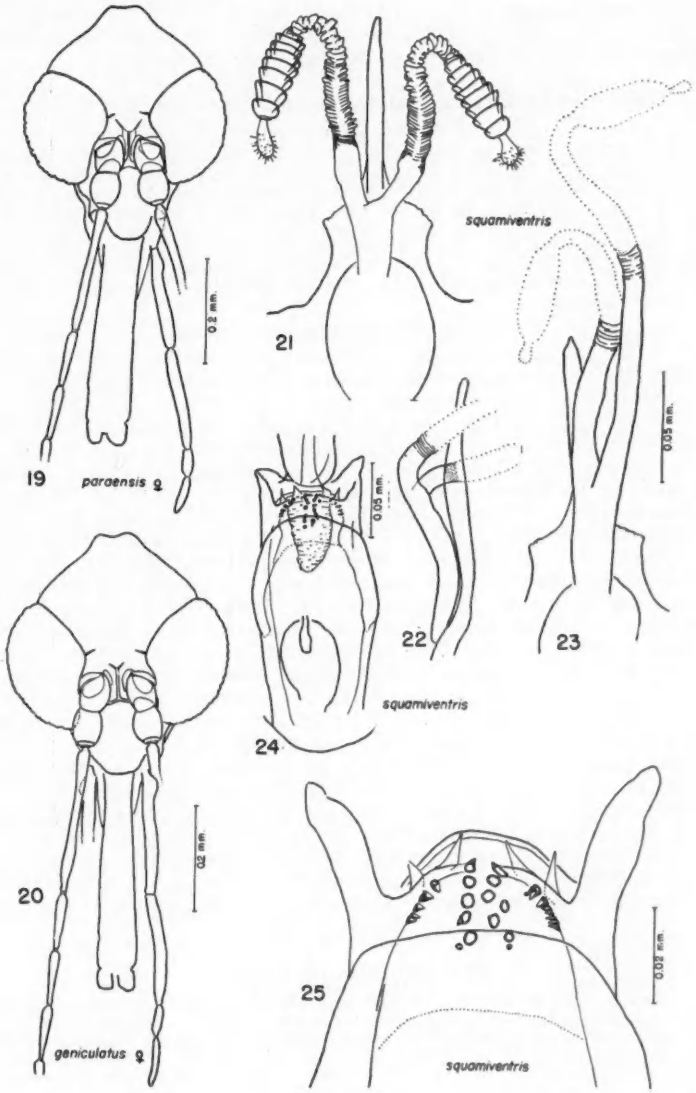
Male genitalia as figured. Dorsal aspect of coxite and style with numerous moderately broad striate scales, and a few such scales scattered along the outer aspect of the lateral lobes. Pump long, the "pavillon" rather small. Genital filaments slender, tips simple, about three times as long as the pump. The genital filaments of this and the following species are sometimes coiled within the base of the genitalia. Female cibarium as figured. Pharynx rather broad and well sclerotized, with fine, transverse, minutely spinulose ridges at its posterior end. Spermathecae as figured. Ninth tergite with numerous ligulate scales mixed with the setae. Stem of genital fork thick and heavy, though not blade-like. Gonapophyses of eighth sternite heavy pointed rods.

The sexes of this species are associated on the basis of colorational and metrical characters and of a single collection of 3 males and 3 females taken at light in a Shannon trap, La Victoria, Cerro Jefe, 1 Sept., 1950, Yellow Fever Station D, 2100 ft. elevation, M. Hertig and P. Galindo colls. The relatively few other *Phlebotomus* taken on this occasion all belonged to unrelated groups. The single specimen previ-

---

EXPLANATION OF PLATE IV

FIG. 19. *P. paraensis*, head, female. FIG. 20. *P. geniculatus*, head, female. FIG. 21. *P. squamiventris*, spermathecae, ducts and genital fork, dorsal aspect. Note that sclerotized portion ends on individual ducts. FIGS. 22, 23. Same, spermathecae stained in phenol after KOH, showing bifurcation of ducts and termination of sclerotized portion; in fig. 23, ducts have been stretched in manipulating specimen. FIG. 24. Same, entire cibarium, female, showing armature, chitinous arch, pigment patch, salivary pump. FIG. 25. Same, cibarium, different female, showing detail of armature, pigment patch omitted.


19
paraensis ♀
0.2 mm.
21
squamiventris
0.05 mm.
22
23
0.05 mm.
24
squamiventris
20
geniculatus ♀
.02 mm.
25
squamiventris
0.02 mm.

ously reported (Fairchild, *l.c.*) as possibly being this species was lost before careful study of it could be made, but in view of the subsequent captures, it is probable that it belonged here. Our males do not differ discernibly from the figures and description of Mangabeira.

Phlebotomus (Shannonomynia) squamiventris Lutz and Neiva

Figs. 3–5, 21–25, 39, 45, 49

1912, Mem. Inst. Oswaldo Cruz, 4 (1): 89 (♀; Rio Trombeta and Para, Brasil). Franca, 1920, Bull. Soc. Portug. Sci. Nat., 8: 225 (♂, ♀; Matto Grosso, Brasil). Costa Lima, 1932, Mem. Inst. Oswaldo Cruz, 26 (1): 23–25, figs. 1, 2, 4, 5, 7, 8, 9, 41, 42, 68, 140, 141. Root, 1934, Amer. Jour. Hygiene, 20: 234–237 (♀; Santarem, Para, Brasil, and Iquitos, Peru). Galvao and Coutinho, 1940, Rev. Ent., 11 (1–2): 434 and figs. Costa Lima, 1941, Acta Medica Rio de Janeiro, 7 (1): 8–14. Floch and Abonnenc, 1944, Inst. Pasteur Guyane, pub. 88, pp. 3–5, fig. 3. Barretto, 1947, Arq. Zool. Est. S. Paulo 5 (4): 224–225.

No species of American *Phlebotomus* seems to have given rise to as much discussion as this one. We have cited above only the more important references, as there seems no point in repeating here the full treatment given by Barretto (*l.c.*).

The material on which we base the following discussion consists of a male and about 50 female specimens, some of which we have mounted, the rest examined in phenol. This series was taken in a donkey-baited stable trap in Villavicencio, Intendencia de Meta, Colombia, 10 June, 1948, by Dr. C. Y. Chow. Dr. Chow informed us that these specimens represented the total catch of *Phlebotomus* in that trap for that night.

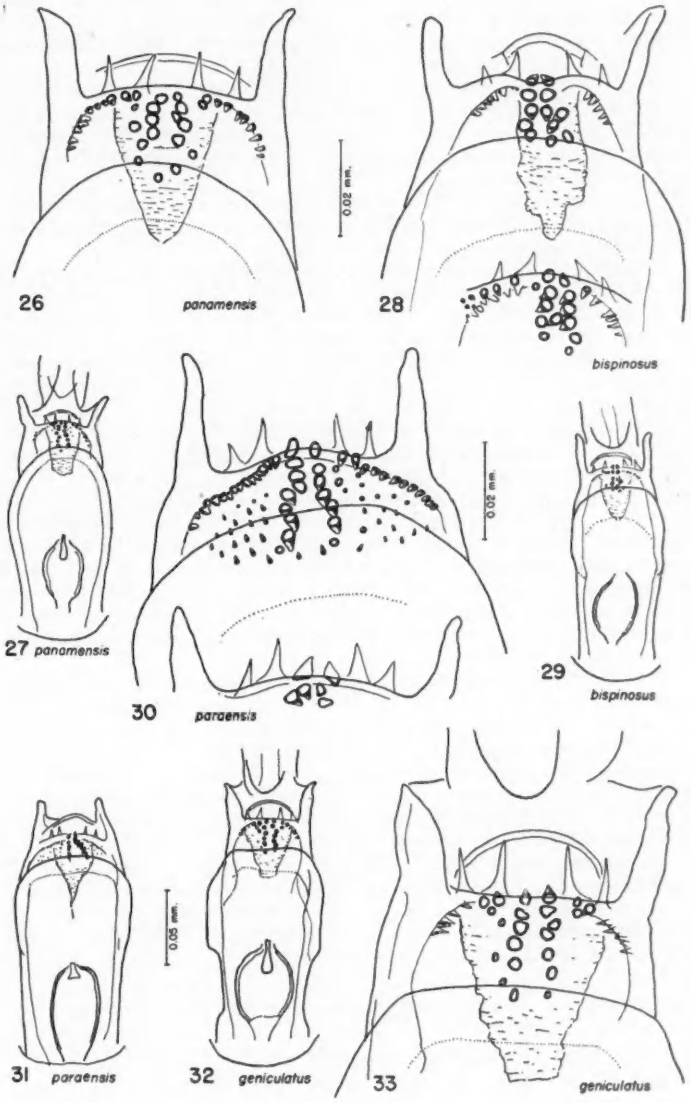
The original description of *squamiventris* by Lutz and Neiva (1912) is, as might be expected, inadequate by present standards, but the types are preserved at the Instituto Oswaldo Cruz. These specimens, all females, were collected on the Rio Trombeta, above Obidos in the State of Pará, by José Diniz and Adolpho Ducke, and another lot of many females was taken in Pará by Dr. Peryassu. The description based on this material was drawn up in December, 1911. Later Lutz and Neiva received additional material from northern Matto Grosso, in part labelled Salto Augusto, and collected by Dr. Murillo de Campos. These specimens consisted of many females and two males, the latter mouldy. Lutz and Neiva identified these as "*squamipennis*," an obvious misprint for *squamiventris*, in an appendix to their paper dated October, 1912, but gave no recognizable description of the male.

In 1919 Bonne-Wepster and Bonne reported the species from Surinam, but we have not seen this publication. Franca (1920) discussed the species and described the male from specimens sent him

---

EXPLANATION OF PLATE V

Female cibarium entire, showing armature, chitinous arch, pigment patch, salivary pump; detail of armature at higher magnification. The central rows or patch of very heavy erect teeth are characteristic of most of the group. FIGS. 26, 27. *P. panamensis*, two different females. FIGS. 28, 29. *P. bispinosus*, two females, with detail of armature of a third. FIGS. 30, 31. *P. paraensis*, three females. A pair of erect teeth sometimes project so that there may appear to be six horizontal teeth, as in detail of armature forming part of fig. 30; pigment patch omitted in latter figure. FIGS. 32, 33. *P. geniculatus*, same female.


0.02 mm.
26 panamensis
28 bispinosus
27 panamensis
30 paraensis
0.02 mm.
29 bispinosus
0.05 mm.
31 paraensis
32 geniculatus
33 geniculatus

by Lutz. This male appears to have been one of the two from Matto Grosso mentioned by Lutz and Neiva in the appendix to their paper. We have not seen this publication, but Costa Lima (1932) has discussed it and reproduced Franca's figure of the style.

Dyar (1939) in discussing the species claimed that the females studied by Franca were *rostrans* Summers, and only the male was *squamiventris*. He claimed to have seen specimens from Venezuela, sex not stated, but presumably males, and states that the fifth palpal segment was very long.

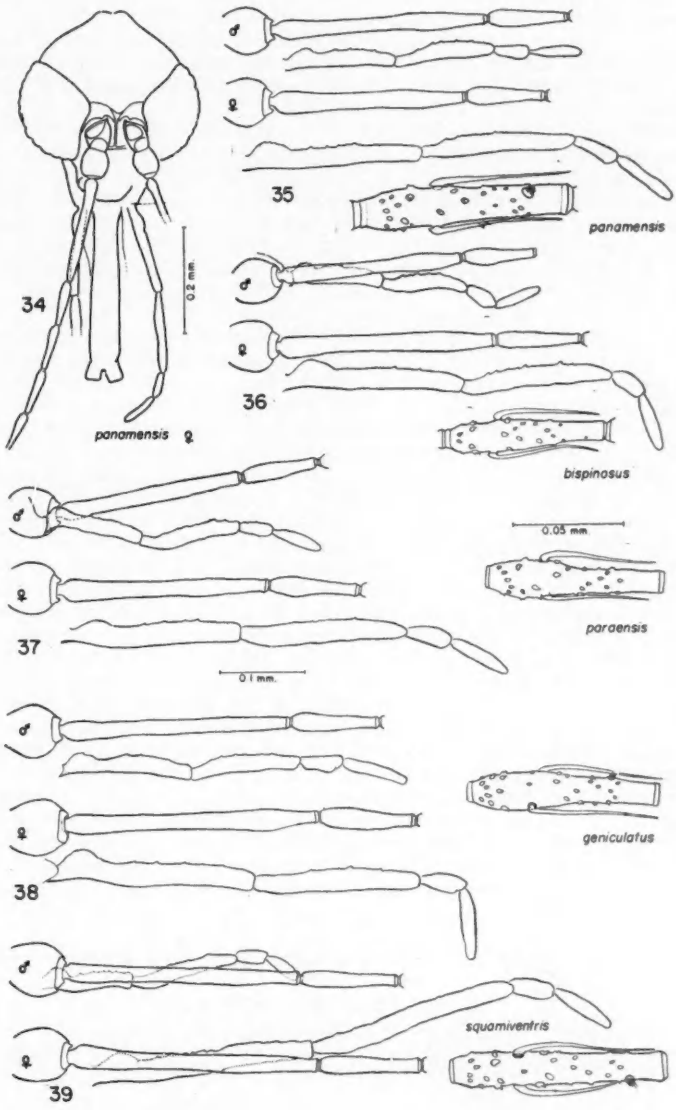
Pinto (1930) reproduced an unpublished figure by Lutz of the male terminalia of *squamiventris* which we have not seen, but which Costa Lima (1932) said agrees with Franca's figure.

In 1932 Costa Lima discussed the species at length after an examination of Lutz and Neiva's material and some additional material from Brasil and Venezuela. He concluded that all the material studied by Lutz and Neiva and by Franca, together with additional material from the Rio Negro collected by Carlos Chagas and from Venezuela, collected by Lutz, appeared to belong to a single species. Dyar's Venezuelan material Costa Lima believed to be *P. evansi* Tovar. He gave figures and measurements of the palpi of females from Matto Grosso, Para, Rio Negro and Venezuela, of the wings of Para and Matto Grosso specimens, and photomicrographs of the spermathecae of two Matto Grosso specimens. These photographs, especially figure 141, show that the sclerotized portion of the individual duct ends abruptly, with the evaginated pouches much compressed, giving the "herringbone" appearance characteristic of all our specimens (our fig. 21). So far as we are aware, in all other species of this group, with the possible exception of Root's species mentioned in the next paragraph, the sclerotization includes the entire length of the individual ducts and usually some of the common ducts as well.

Root (1934), treating the *Phlebotomus* with short fifth palpal segment, notes that the male described by Franca has palpi very different from the female and doubts that they are conspecific, but unlike Dyar, he realized that the name must be based on the female. He determined as *squamiventris* a female from Santarem, Para, and 8 females from Iquitos, Peru. He gave figures of palpi, cibarium, pharynx and spermathecae, unfortunately not stating whether they were made from the Para or Iquitos specimens. He was unable to see the bifurcation of the spermathecal ducts. This fact strongly indicates that the sclerotization did not extend to the bifurcation, a striking and uncommon character in this group. However, the rather slender ducts and their irregular coarse annulations do not correspond with the "herringbone" pattern of Costa Lima's and our specimens.

EXPLANATION OF PLATE VI

FIG. 34. *P. panamensis*, head, female. FIGS. 35–39. Antennal segments II–IV and palps, male and female, drawn to same scale; antennal segment IV with ascoids enlarged: fig. 35, *P. panamensis;* fig. 36, *P. bispinosus;* fig. 37, *P. paraensis;* fig. 38, *P. geniculatus;* fig. 39, *P. squamiventris.*


34
0.2 mm.
panamensis ♀
35
panamensis
36
bispinosus
0.05 mm.
37
paraensis
0.1 mm.
38
geniculatus
39
squamiventris

Galvao and Coutinho (1940) gave keys to males and females of the species of *Phlebotomus* then known from Brazil. The characters for the male appear to be those used by Franca (1920) and Costa Lima (1932), while the characters for the female were based on material presumably from Sao Paulo. The spermatheca of the female is figured in both a drawing and a photomicrograph.

Floch and Abonnenc (1944) gave descriptions and figures of what they considered *squamiventris*, based on females from French Guiana.

Costa Lima reviewed the problem again in 1941 and came to the conclusion that the types of *squamiventris* must be restricted to Lutz and Neiva's specimens from Para, that some of their females from Matto Grosso may be small specimens of *squamiventris*, but that those labelled "Salto Augusto" are a different species. The specimen from Rio Negro formerly (1932) considered by him to be *squamiventris*, he believed in the later paper (1941) to be different and named it *P. chagasi*, while Root's *squamiventris* he also believed to have been based on one or more different species. The Venezuelan specimen referred to *squamiventris* in 1932 he later considered to be *panamensis*. Costa Lima placed great emphasis on the lengths, both actual and relative, of the palpal segments and gave charts of palpal lengths of various specimens. It should be noted that the figures for palpal segments IV and V in this paper (1941) are reversed. The explanation of the figures would result in IV being longer than V, which is never so in this group.

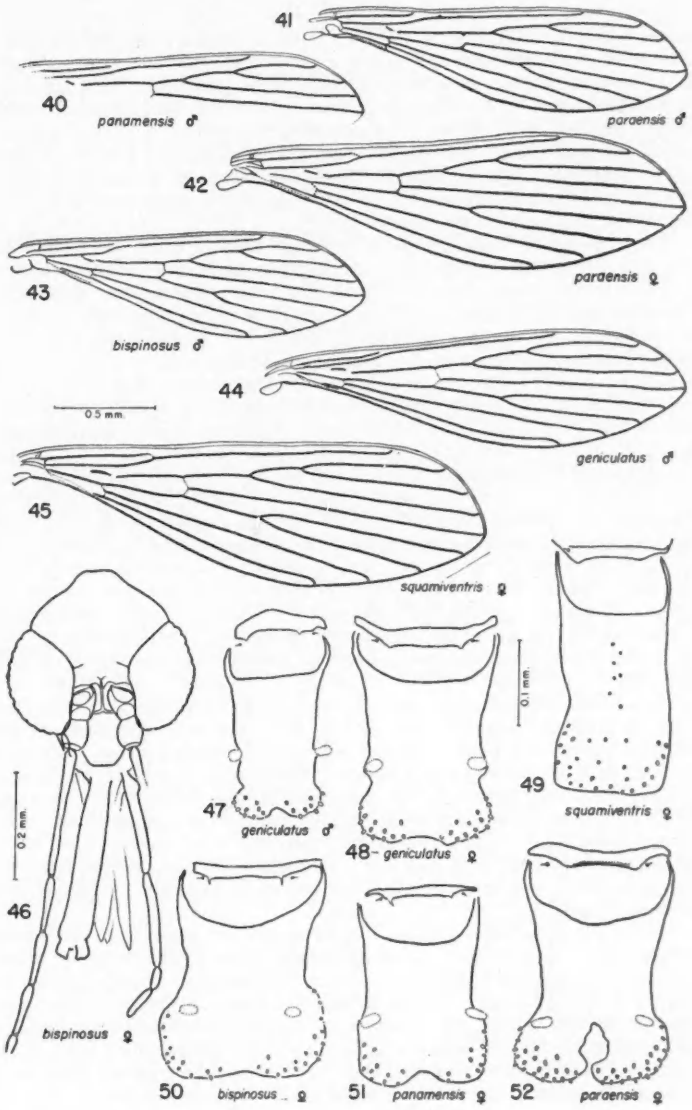
We have compared our female specimens with all the foregoing descriptions and figures and have concluded that they agree only with the specimens from Matto Grosso discussed by Costa Lima and considered by him to be probably small specimens of *squamiventris*. The palpi of our material range in total length, excluding the first segment for comparison with Costa Lima's measurements, from 522 micra to 586 micra. He gave 535 micra for the Matto Grosso specimens and 645 micra for those from Para. The length and character of the spermathecal ducts and the structure of the cibarium seem to us of utmost importance in this group, but unfortunately adequate descriptions or figures of these structures have not been given for true *squamiventris* from Para, for *chagasi* or for the other material discussed by Costa Lima. Root also was unable to make out the non-sclerotized parts of the ducts in his material. The portions of the ducts which he did see, however, are quite different from the comparable parts in our material. Root also stated that the pigmented patch in the cibarium of his specimens was faint or absent, while it is quite strongly marked in ours.

EXPLANATION OF PLATE VII

FIGS. 40–45. Wings: fig. 40, *P. panamensis*, male, costal portion; figs. 41, 42, *P. paraensis*, male and female; fig. 43, *P. bispinosus*, male; fig. 44, *P. geniculatus*, male; fig. 45, *P. squamiventris*, female.

FIG. 46. *P. bispinosus*, head, female.

FIGS. 47–52. Sternites I and II: figs. 47, 48, *P. geniculatus*, male and female; fig. 49, *P. squamiventris*, female; fig. 50, *P. bispinosus*, female; fig. 51, *P. panamensis*, female; fig. 52, *P. paraensis*, female.


41
40
panamensis ♂
paraensis ♂
42
pardensis ♀
43
bispinosus ♂
0.5 mm.
44
geniculatus ♂
45
squamiventris ♀
0.2 mm.
46
bispinosus ♀
47
geniculatus ♂
48- geniculatus ♀
0.1 mm.
49
squamiventris ♀
50
bispinosus ♀
51
panamensis ♀
52
paraensis ♀

The species whose spermathecae are figured by Galvao and Coutinho (1940) is obviously quite different, with much shorter, entirely sclerotized, individual ducts. Their figures, especially the photograph, show both spermathecae and ducts in their general form, proportions and sclerotization, to be very closely similar to ***geniculatus*** (our fig. 15). Floch and Abonnenc's (1944) figures are unfortunately printed on such poor paper that it is difficult to be sure of the character of the sclerotization of the ducts or of the number and arrangement of the erect spines in the cibarium. The measurements of the palpi and wing which they gave fit well with ***squamiventris*** and we believe it quite probable that they were dealing with true ***squamiventris***.

The associated male we place here on the basis of the collecting data, the similarity of coloring and palpal formula, and the possession of an equally long delta. The only other species of American ***Phlebotomus*** with similar palpi, coloring, and wing venation are ***unisetosus*** Mang. and ***complexus*** Mang., both known only in the male sex. Our male is exceedingly close to ***complexus***, differing only in details of the parameres. It is quite possible, of course, and indeed very likely, that ***complexus*** is in reality the male of ***squamiventris***, since both were from near Belem, Para, and that our species is a closely allied form, perhaps ***chagasi*** C. L. In view of the close similarity of the females of this group it may prove impossible to find characters to differentiate the females of ***complexus***, ***unisetosus*** and ***squamiventris***. Lacking material of either ***complexus*** or ***squamiventris*** from near the type locality, and in view of the differences in our single male from the description of ***complexus***, we hesitate to synonymize the two species. Although realizing that our male is distinct from any described species, the close correspondence of the associated females with ***squamiventris*** make it seem undesirable to erect a new name until the related species are better known. For purposes of comparison we give here a description and figure of our material.

A medium sized sandfly with conspicuously infuscated mesonotum. Eyes of average size for the genus. Tergites and sternites, except margins, apparently clothed largely with broad striated scales. Margins clothed with semi-recumbent setae. Wings with venation as figured, clothed with long hairs and at least some lorate striate scales at base. Palpi as figured, those of the female nearly twice as long as those of the male. Newstead's scales sparsely scattered over nearly the whole dorsal aspect of the third segment. Ascoids as figured, absent from the terminal three segments in the female, not certainly visible in the unstained male.

Male genitalia as figured. Dorsal aspect of style with numerous non-deciduous lorate scales, not all shown in our figure, a few of which appear to have been present on the coxite also. Pump large, the filaments slender, twice coiled within the base of the genitalia, their tips not clearly visible, but apparently somewhat inflated and annulate just before the tip. Filaments twice or somewhat less the length of the pump. Female cibarium as figured. Pharynx rather broad, with weak digitate processes at the posterior end. Spermathecae as figured. Ninth tergite with mixed lorate scales and setae. Gonapophyses of eighth sternite slender with somewhat falcate tips. Stem of genital

fork slender but blunt. Cerci of male rather slender and pointed, of female broader but quite acute.

REFERENCES

Barretto, M. P. 1946. Uma nova espécie de flebótomo da Colombia e chave para a determinacao das espécies afins. An. Fac. Med. Univ. S. Paulo, 22: 279–293.

1947. Catalogo dos flebótomos americanos. Arq. Zool. Est. S. Paulo, 5 (Art. 4): 177–242.

Bonne-Wepster, J., and **Bonne, C.** 1919. Een *Phlebotomus* soort in Suriname, *Phlebotomus squamipennis* Lutz and Neiva. Batavia Geneesk. Tydschr. Ned.-Ind., 59: 676–680.

Costa Lima, A. da. 1932. Sobre os phlebotomos americanos. Mem. Inst. Oswaldo Cruz, 26 (1): 15–69, 152 figs.

1941. Um novo *Flebotomus* da Amazonia e consideracoes relativas as espécies afins. Acta Medica, Rio, 7 (1): 3–19, 1 plate, 4 text figs.

Dyar, H. G. 1929. The present knowledge of the American species of *Phlebotomus*. Amer. Jour. Hygiene, 10: 112–124.

Floch, H., and **Abonnenc, E.** 1944. Phlébotomes de la Guyane Francaise. (X) Sur les femelles a 5e segment des palpes court. Inst. Pasteur de la Guyane, Pub. No. 88, pp. 3–5, fig. 3.

Franca, C. 1920. Observations sur le genre *Phlebotomus*. II. *Phlebotomus* du Nouveau Monde (Phlébotomes du Brésil et du Paraguay). Bull. Soc. Portug. Sc. Nat., 8: 215–236.

Galvao, A. L. A., and **Coutinho, J. O.** 1940. Contribuicao ao estudo dos flebotomos de Sao Paulo. Dipt. 1a nota. Rev. Ent. 11 (1–2): 434, 435, fig. 14 and plate 16, fig. 9.

Mangabeira, O. 1942. 7a contribuicao ao estudo dos *Flebotomus*. Mem. Inst. Oswaldo Cruz, 37 (2): 119.

Mangabeira, O., and **Galindo, P.** 1944. The Genus *Flebotomus* in California. Amer. J. Hygiene, 40: (2): 190.

Pinto, C. 1930. Arthropodos parasitos e transmisores de doencas. Tomo II. Biblioteca Scientifica Brasileira, pp. 491–538.

Root, F. M. 1934. Some American species of *Phlebotomus* with short terminal palpal segments. Amer. Jour. Hygiene, 20: 233–246, 5 figs.

Sinton, J. A. 1925. Notes on some Indian species of the genus *Phlebotomus*. Part XIV. The hypopygium of the female *Phlebotomus*. Indian Jour. Med. Res., 13 (1): 100.

NOTES ON THE PHLEBOTOMUS OF PANAMA

(Diptera, Psychodidae)

VIII. Two New Species of Warileya[1]

G. B. FAIRCHILD and MARSHALL HERTIG
Gorgas Memorial Laboratory,
Panama, R. de P.

It has been believed until quite recently that all the bloodsucking Psychodidae belong to the genus *Phlebotomus*. This genus is considered by Theodor (1948) to form the subfamily Phlebotominae, although Eaton (1904) and some earlier authors included *Nemopalpus*, *Sycorax* and *Trichomyia* in the subfamily as well. The haematophagous habit and its concomitant structural modifications, however, are not limited to this group, as Desportes (1942) has shown that *Sycorax silacea* feeds on frogs and is actually a vector of a frog filaria. *Horaiella*, a genus described by Tonnoir (1933) as having toothed mandibles in the female, may also possibly be haematophagous, although it does not bite man. Neither of these genera are believed by Tonnoir to belong in the Phlebotominae. More recently Hertig (1948) has described *Warileya phlebotomanica* from Peru, an avidly haematophagous species, while Fairchild (1949) in describing *Hertigia hertigi* from Panama indicated that the structure of the mouth parts of the single available specimen, a male, suggests a possible bloodsucking habit.

It is of some interest, therefore, to add two more species to *Warileya*, one of which at least is a feeder on human blood. The inclusion of these two additional species necessitates a re-characterization of *Warileya*, as some of the more outstanding characters of the type species are lacking in the present forms, and hence appear to be only of specific value. We were long doubtful of the proper placement of these two species and it may yet be necessary to place the second species elsewhere. Short of erecting new genera for them, however, we see no alternative to placing them in *Warileya*.

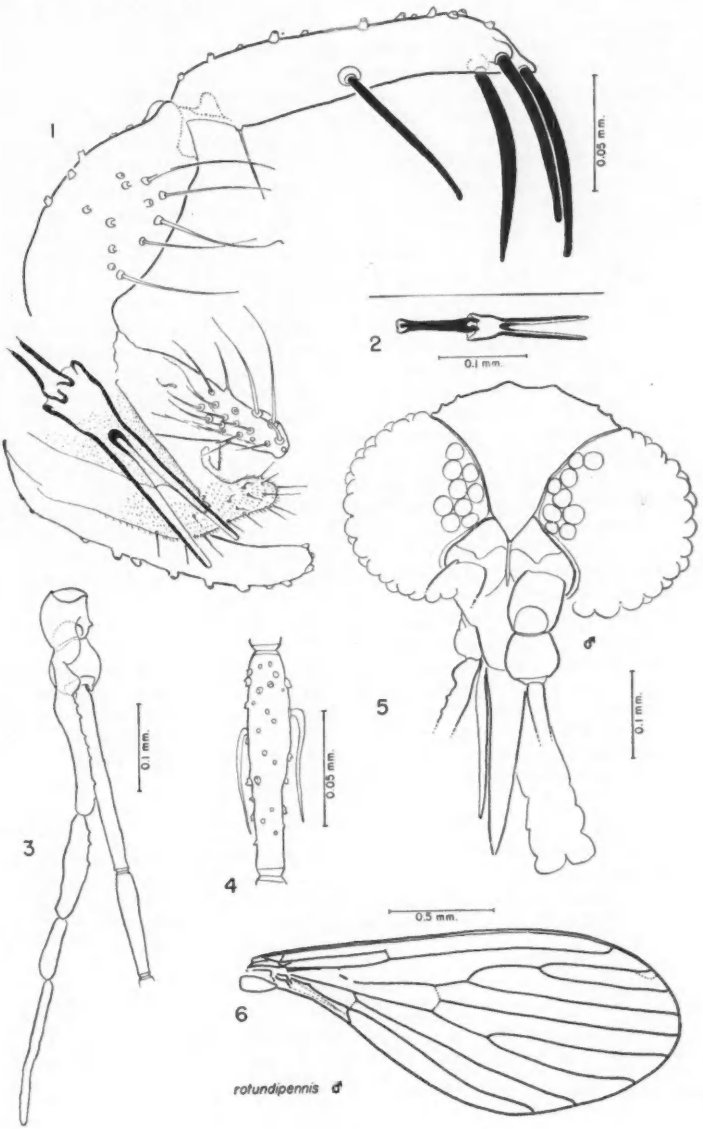
Warileya differs from *Phlebotomus* sensu lato in possessing the following combination of characters: A very broad and rounded wing, the ratio of length to width ranging from 2.2 to 2.7, alpha and delta

[1]Cost of publication is paid by the Gorgas Memorial Institute.

EXPLANATION OF PLATE I

All drawings for this and other plates were made by the authors with the aid of the camera lucida from stained copal-balsam preparations, except as noted. Magnifications are indicated on the drawings.

Warileya rotundipennis, paratype males. Fig. 1. Male genitalia, inner aspect. Fig. 2. Pump and genital filaments. Fig. 3. Palp and antennal segments I-IV. Fig. 4. Antennal segment IV, with ascoids. Fig. 5. Head. Fig. 6. Wing.


1
0.05 mm.
2
0.1 mm.
3
0.1 mm.
4
0.05 mm.
5
♂
0.1 mm.
0.5 mm.
6
rotundipennis ♂

very long, gamma very short. The wing of *Phlebotomus* is relatively slender and is usually pointed. In fifteen Panamanian species selected at random except for two species with very narrow wings, the ratio of length to width ranged from 2.85 to 4.7, with an average of 3.5. No definite armature of teeth in the cibarium in either sex. This character is shared by many Old World species of *Phlebotomus*, but by none in the New World. The species of *Brumptomyia* are often stated to have a "rudimentary" armature, but actually they have quite large teeth set in longitudinal rows. Male genitalia with the coxite short and broad, much shorter than the style. Style long and cylindrical, bearing up to four strong spines. Parameres simple. Aedeagus conspicuously divided, the genital filaments short, not exceeding twice the length of the genital pump. Lateral lobes unarmed, hardly exceeding the parameres in length. The relatively short and broad coxite is approached only by certain species of the subgenus *Shannonomyina* Pratt, which are otherwise quite different. In other respects the genitalia are not very distinctive, the remarkable development of modified setae on the coxite of *W. phlebotomanica* apparently being only a specific character. Spermathecae quite unlike in the three included species, opening by separate ducts into the vagina in two species, into a short common duct in the third. Genital fork with a rounded, flattened terminal expansion in at least two of the species, and all three with a pair of internal sclerotized flattened rods apparently arising near the bases of the lobes of the eighth sternite and passing forward ventral to the genital fork. These latter structures are present in most *Phlebotomus*, though much less developed in the species we have examined, where they vary in shape from species to species. These structures appear to be what Sinton (1925) believed are probably the gonapophyses of the eighth segment.

The thorax differs from *Phlebotomus* in lacking setae on the upper part of the anepisternum, these being present in all species of *Phlebotomus* we have seen. The abdomen is sparsely clothed with relatively long and stout erect hairs in two of our species, the third having much more numerous and finer setae which tend to be recumbent and many of which are scale-like.

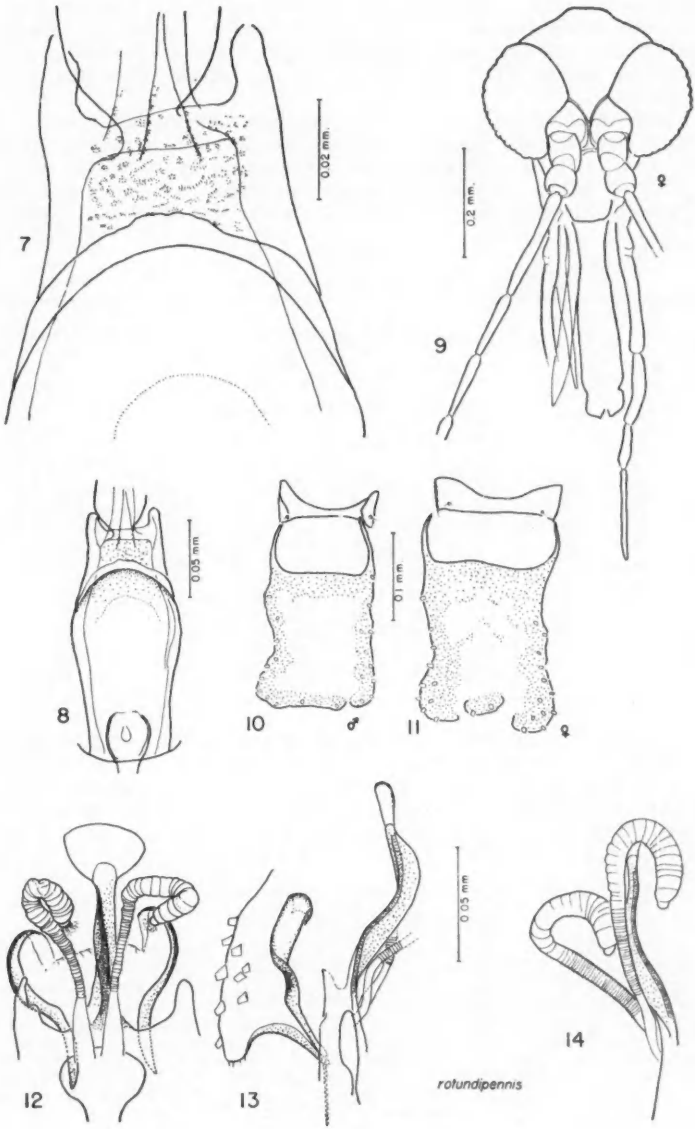
Warileya rotundipennis sp. nov.

A medium sized, entirely pale colored insect closely resembling *Plebotomus* in appearance, stance and flight habits. Vestiture of wings moderately dense, wholly of slender hairs, without admixture of scales. Venation as figured. Thorax as in *Phlebotomus*, but lacking

---

EXPLANATION OF PLATE II

W. rotundipennis; Figs. 7, 8, 9, 12, allotype female, other figures paratypes. FIGS. 7–8. Cibarium. Note absence of true armature; ventral wall studded with groups of minute spinules; chitinous arch with irregular flange-like posterior projection. FIG. 9. Head. FIGS. 10–11. Sternites I and II, male and female. FIG. 12. Spermathecae, genital fork, gonapophyses of eighth sternite, dorsal aspect. FIG. 13. Genital fork, gonapophyses, bases of spermathecal ducts, lateral aspect. FIG. 14. Spermathecae, after KOH, stained, in phenol.


7
0.02 mm.
9
0.2 mm.
♀
8
0.05 mm
10
♂
0.1 mm
11
♀
12
13
0.05 mm
14
rotundipennis

setae on the upper margin of the anepisternum (postspiracular setae). Legs as in *Phlebotomus*, without spines on femora, and rather uniformly and densely clothed with lanceolate ribbed scales. Abdomen with relatively sparse, stout, erect setae, without scales. Second sternite as figured.

Male genitalia as figured. The aedeagus is poorly sclerotized and rather membranous, the pump and genital filaments unusually short, as figured. Head as figured, with very large eyes, especially in the male, the suture defining the upper border of the antennal plates Y-shaped in both sexes. Proboscis and clypeus well developed, together

TABLE I

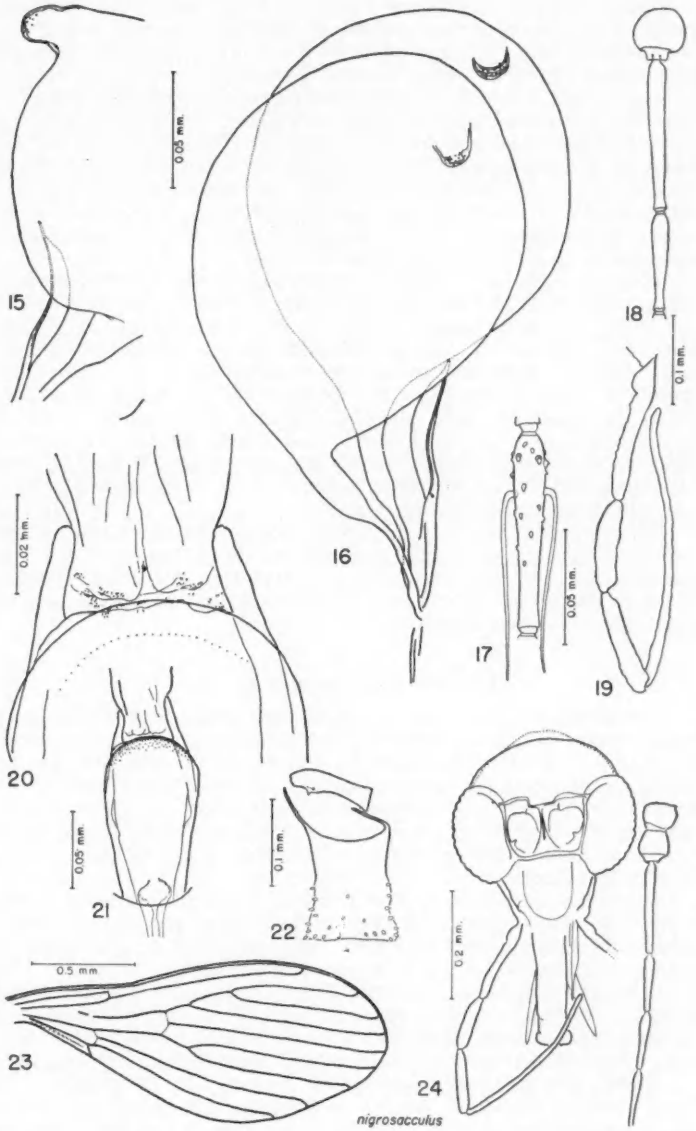
MEASUREMENTS IN MICRA

	Warileya rotundipennis (6 ♂, 6 ♀ measured)						*W. nigrosacculus* (1 ♀)
	Maximum		Minimum		Mean		
	♂	♀	♂	♀	♂	♀	
Ant. III	224	240	192	216	204	224	176
Palpi I-II	176	244	164	224	168	232	156
" III	128	176	98	136	115	133	104
" IV	76	92	64	80	66	86	116
" V	168	192	140	156	155	173	316
Wing, length	2160	2286	1962	2196	2052	2255	1890
Alpha	576	720	504	612	533	641	576
Beta	360	360	306	324	365	333	198
Gamma	144	162	126	90	126	137	126
Delta	378	450	288	360	333	410	342

greater than the distance from base of clypeus to vertex in both sexes. Antenna of 16 segments, the terminal segments not abruptly shorter. Ascoids long, as in *Phlebotomus*, paired on all flagellar segments in the female, apparently lacking or much reduced on last four segments of male. Newstead's scales in a rather dense patch just beyond the middle of the third palpal segment in both sexes.

EXPLANATION OF PLATE III

W. nigrosacculus, holotype female. FIGS. 15–16. Spermathecae. FIG. 16, unstained, in phenol, lateral aspect; the "terminal knobs," both on inner surfaces, are irregularly thickened evaginations of the thin wall of the bladder-like spermathecae. After treatment in KOH (fig. 15) one terminal knob seen in profile; tiny refractive dots may indicate bases of "hairs" usually present in *Phlebotomus*. FIG. 17. Antennal segment IV, with ascoids. FIG. 18. Antennal segments II-IV. FIG. 19. Palp. FIGS. 20–21. Cibarium. No true armature, but ventral wall with groups of minute spinules. Chitinous arch with irregular flange-like posterior projection; this part of specimen foreshortened downward from plane of drawing. FIG. 22. Sternites I and II. FIG. 23. Wing. FIG. 24. Head. Specimen somewhat flattened in mounting; probable outline of vertex dotted.


0.05 mm.
15
16
18
0.1 mm.
0.02 mm.
17
0.05 mm.
19
20
0.05 mm.
21
0.1 mm.
22
0.5 mm
23
0.2 mm.
24
nigrosacculus

Female cibarium as figured, without a true armature, but with scattered groups of minute spinules on the membranous ventral wall of the cibarium. Chitinous arch with irregular flange-like posterior projection. Pharynx quite heavily sclerotized and dark colored, without spines, but with ridges and digitate processes which may be minutely spinulose. Spermathecae as figured, the walls lacking the imbricated and heavily sclerotized character of portions of the ducts as found in *W. phlebotomanica*, and lacking the elongate terminal knob. Genital fork in dorso-ventral view with the anterior stem ending in a flattened disc. Gonapophyses of the eighth sternite (Sinton), broad, curved, strap-like sclerotizations in lateral view, slenderly S-shaped in dorsal view. Cerci short and slender.

Holotype male, slide 2335, *allotype* female, slide 2312; 5 *paratype* males, slides 2336 to 2340, and 5 *paratype* females, slides 2309 to 2311 and 2313–2314; 13 *paratype* males in alcohol; Cerro Campana, Panama Province, Panama, 24 August, 1950, M. Hertig and G. B. Fairchild colls.; taken at lighted Shannon trap in dense forest at Yellow Fever Station F, 1900 ft. elevation, the allotype and 3 other females taken biting the collectors. The latter four females all had partly developed eggs, indicating a previous blood meal. One paratype male, slide 2389, La Victoria, Cerro Jefe, Panama Province, 29 August, 1950, M. Hertig and P. Galindo colls.; taken at light, Shannon trap, Yellow Fever Station C, 1200 ft. elevation.

This species differs from *W. phlebotomanica* Hertig in smaller size, relatively shorter fifth palpal segment, and in characters of the male genitalia and spermathecae. From *W. nigrosacculus* n. sp. it differs in larger size, much shorter fifth palpal segment, larger eyes, and the very different spermathecae.

Warileya nigrosacculus sp. nov.

A small dusky insect with unusually dark integument. Vestiture of wings moderately dense, of slender, lorate or narrowly lanceolate scale-like hairs. Venation as figured. Thorax as in *Phlebotomus*, but lacking post-spiracular setae. Legs as in *Phlebotomus*, the femora unarmed, clothed with striate scale-like hairs. Abdomen densely clothed with recumbent or semi-recumbent fine setae, those of the venter at least lorate or narrowly lanceolate and scale-like. Second sternite as figured.

Spermathecae relatively enormous, thin-walled balloon-like structures, their ducts fusing very close to the vagina, as figured. Stem of genital fork simple, not expanded. Gonapophyses of eighth sternite simple curved rods. Cerci rather small and slender.

Cibarium without true armature but with scattered groups of minute spinules on ventral wall. Pharynx broad and rather strongly pigmented, quite smooth except for a few wrinkles at the extreme posterior end. Eyes rather small. Proboscis and clypeus relatively long.

Newstead's scales in a small patch proximal to the middle of the third antennal segment. Ascoids long and slender, exceeding the ends of their respective segments, but apparently absent from the six terminal segments.

Holotype, slide 705, Cerro Campana, Panama Province, Panama, 7 January, 1947, M. Hertig coll. Taken from a hollow tree in heavy wet forest at about 3000 ft. elevation. Although this area and the tree where this specimen was taken have been visited on numerous subsequent occasions, no other specimen has been collected.

This species differs markedly from the other species of *Warileya* in the structure of the spermathecae and character of the vestiture. It is so similar in wing and head characters, however, that we believe it is best placed here, at least until the male can be studied.

REFERENCES

Desportes, C. 1942. *Forcipomyia velox* Winn. et *Sycorax silacea* Curtis, vecteurs d'*Icosiella neglecta* Diesing, filaire commune de la grenouille verte. Ann. Parasit. Hum. Comp. 19 (1–3): 53–68, 5 figs.

Eaton, A. E. 1904. New genera of European Psychodidae. Ent. Month. Mag., Ser. 2, 15: 55–59.

Fairchild, G. B. 1949. A new fly related to *Phlebotomus* from Panama. Proc. Ent. Soc. Washington, 51 (2): 81–84, 5 figs.

Hertig, M. 1948. A new genus of bloodsucking psychodids from Peru. Ann. Ent. Soc. Amer., 41 (1): 8–16, 1 fig., 2 plates.

Sinton, J. A. 1925. Notes on some Indian species of the genus *Phlebotomus*. Part XIV. The hypopygium of the female *Phlebotomus*. Ind. Jour. Med. Res., 13 (1): 97–108, 2 plates.

Theodor, O. 1948. Classification of the Old World species of the subfamily Phlebotominae (Dipt. Psychodidae). Bull. Ent. Res., 39 (1): 85–115, 15 figs, 1 plate.

Tonnoir, A. L. 1933. Descriptions of remarkable Indian Psychodidae. Records. Ind. Mus., 35: 53–75, 7 figs. and Plate II.

THE IMMATURE STAGES OF CULICOIDES TRISTRIATULUS HOFFMAN

(Diptera, Heleidae)

ROGER W. WILLIAMS[1]

School of Public Health of the Faculty of Medicine,
Columbia University

The members of the haemophagous genus *Culicoides* are of considerable concern to medical entomologists because of their economic and medical importance. Many regions of the world, including arctic regions as well as warmer areas, are rendered almost uninhabitable because of their painful bites. They have been shown to be the probable vectors of several species of filariid worms of man and horses (Buckley, 1934, 1938; Sharp, 1928; Steward, 1933) and may be involved in the transmission of other diseases. The literature concerning adult taxonomy and morphology is relatively voluminous in contrast to the paucity of the treatises pertaining to the morphology of the immature stages. A comprehensive discussion of this subject with full bibliography is presented by Hill (1947) and Fox (1942). It is apparent that there exists very little information concerning the immature forms of species found in the Nearctic realm since little effort has been made to associate these forms with their respective adults.

Culicoides tristriatulus has been reported, according to Dr. W. W. Wirth of the U. S. National Museum (personal communication), from Cook Inlet, Kodiak, Pigot Bay, Goose Bay, Anchorage, and Valdez in Alaska, and Eureka, Mill Valley, and Tocaloma in California. Its distribution may include most of the west coast of North America. At Valdez, which is one of the two seaports from which materials are transported into the interior of Alaska, this fly is at times so numerous as to prohibit the unloading of ships.

It is the purpose of this paper to describe the egg, larva, and pupa of *C. tristriatulus* which were first associated with the adult by the author in 1949 through rearing techniques (Williams, 1951). Comparisons are made between the immature stages of this species and illustrations of the same stages of other species to indicate morphological differences which might possibly be useful in developing keys to the immature forms of the genus *Culicoides*. It is recognized, however, that when actual specimens are compared perhaps some structures which are now designated as being of possible taxonomic value will be found to be otherwise. All observations were made on unmounted specimens which could be dissected, manipulated or turned in any direction. The dissected parts were placed in a drop of glycerin under a No. 1 cover slip and studied with oil immersion when necessary. On occasion 18 x oculars were used. Since many structures on the

[1]Material for this study was collected during the summer of 1949 at Valdez, Alaska, while serving as Special Consultant, Alaska Health and Sanitation Activities, U. S. Public Health Service, Anchorage, Alaska. Specimens are now in the U. S. National Museum, Washington, D. C.

body wall of the pupae were much easier to see on the exuviae than on specimens from which the adults had not emerged, the cast skins were used for study.

Egg.—The eggs of *C. tristriatulus* have an average length of about 460 μ and an average width, at the widest point, of 71 μ. Their color is white when deposited but becomes a dark black in a short period of time. They are somewhat fusiform in shape but are slightly more pointed at the posterior end. Hill (1947), Parker (1950), and others have described on the chorion of eggs of several species of *Culicoides* stalked sucker-like structures which in some species appear in definite rows and are thought to act as floats. The biology of *C. tristriatulus* is such that egg floats would appear to be detrimental to the species since they would permit the eggs to be carried from the breeding areas by tidal action (Williams, 1951). No such sucker-like structures are evident, however, there are very short blunt protuberances of varying diameters scattered indiscriminately over the surface (fig. 1).

Larva.—Within 24 hours of hatching the newly emerged larvae varied in size from 669 μ x 75.6 μ, with a head capsule measurement of 75.6 μ x 64.8 μ, to 842 μ x 86.4 μ, having a head capsule size of 108 μ x 75.6 μ. Whether there is a moult within a few hours of hatching or whether an individual variation of this magnitude exists is not known.

When mature, the larvae of *C. tristriatulus* vary in length from 5.2 to 6.1 mm. and are white or creamy while in color with rather heavily sclerotized heads which are yellowish-brown to dark brown. The head is followed by a short cervical region, three thoracic and nine abdominal segments. In 98 specimens the heads measured from 281 to 346 μ in length. The modal length, which occurred in 35 specimens, was 292 μ while the average length was 307 μ. The width of the heads varied from 205 μ to 212 μ at the posterior angle. Each eye-spot consists of a small anterior and larger posterior mass of pigment. The location may vary considerably. Carter *et al.* (1920) indicate that the eye spots of *C. accraensis* move caudally as the larvae approach pupation, a phenomenon which may occur in all species of *Culicoides*. The antennae are closely associated with the dorsal articulations of the mandibles (figs. 5 and 6) and are represented by a number of membraneous lobes or sensilla, the most anterior of which is considerably broader and somewhat longer than the remainder. The number of smaller sensilla is variable, usually ranging between 6, which occurred most frequently, and 10. The right and left antenna of the same larva may bear a different number. The head is divided dorsally by sutures into three plates along which rupture occurs at the time of pupation. These plates have been designated by some investigators as the clypeal, which is the median plate, and the epicranial, which are the two lateral plates. Several pairs of setae and sensory pits are arranged along the sutures and on the lateral and ventral surfaces of the head. These setae may be of value taxonomically since it is evident from the illustrations of the larvae of *C. accraensis* Carter, Ingram, & Macfie (Carter *et al.*, 1920), *C. dovei* Hall (Dove *et al.*, 1932), *C. circumscriptus* Kieffer (Tokunaga, 1937), *C. impunctatus* Goetghebuer (Hill, 1947) and from the study of *C. tristriatulus* that differences do exist between these

species. On the dorsal surface of the head of *C. tristriatulus* (fig. 2), two pairs of minute setae occur near the caudal margin of the epicranial plates and two pairs of large bristles are situated cephalolaterad to them on the edge of the epicranial plates. Between these setae and the eye spots lies a pair of sensory pits (so called by Tokunaga, 1937). Located just anterior to the eye spots are two pairs of large setae, the caudal pair arises on the clypeal plate and the cephalic pair on the epicranial plates. Anterior to this last pair of setae lies another pair of sensory pits. Cephalad another pair of large setae occur on the clypeal plate and two pairs just in front of the antennae, the anterior and ventral pair being somewhat longer. A third pair of sensory pits lies mesad to the antennae (fig. 6). Ventrally the head bears three pairs of large setae (figs. 3, 4) one situated approximately halfway along the length of the head and the other two pairs situated near the cephalic margin of the head. A pair of sensory pits lies dorsad to the latter two pairs of setae. Laterally there are three pairs of large bristles, situated as shown in fig. 4. A pair of sensory pits are located dorsocaudad to the most posterior of these hairs.

The more obvious differences in the number and location of these head setae between the five species mentioned are: (1) the complete absence or the presence of either one or two setae just in front of the antennae; (2) the presence of either three or of four setae on the lateral surface; (3) the presence or absence of a pair of minute setae on the ventrocaudal portion of the head; (4) the location of the setae on the dorsal surface in relation to the dorsal sutures, there being no setae on the clypeal plate of *C. accraensis*. Tokunaga (1937), the only one of the authors cited that mentions sensory pits, states that their position is characteristic for the species. The position of the pits on *C. circumscriptus* as described and illustrated by him and those of *C. tristriatulus* appears approximately the same, however, a fifth pair of pits was found in *C. tristriatulus* mesad to the antennae (fig. 6). Tokunaga (1937) indicated a pair of minute trichoid sensilla at this location in *C. circumscriptus*.

The mandible appears to be a structure which holds promise of offering characters for specific diagnosis. Hill (1947) illustrated the mandibles of five different species (*C. impunctatus*, *C. obsoletus*, *C. odibilis*, *C. pallidicornis*, *C. cubitalis*), all of which are different in shape from each other and all are quite distinct from *C. circumscriptus* as illustrated by Tokunaga (1937) and from *C. tristriatulus*. The mandible of *C. tristriatulus* (fig. 5) possesses a distinct bluntly-rounded,

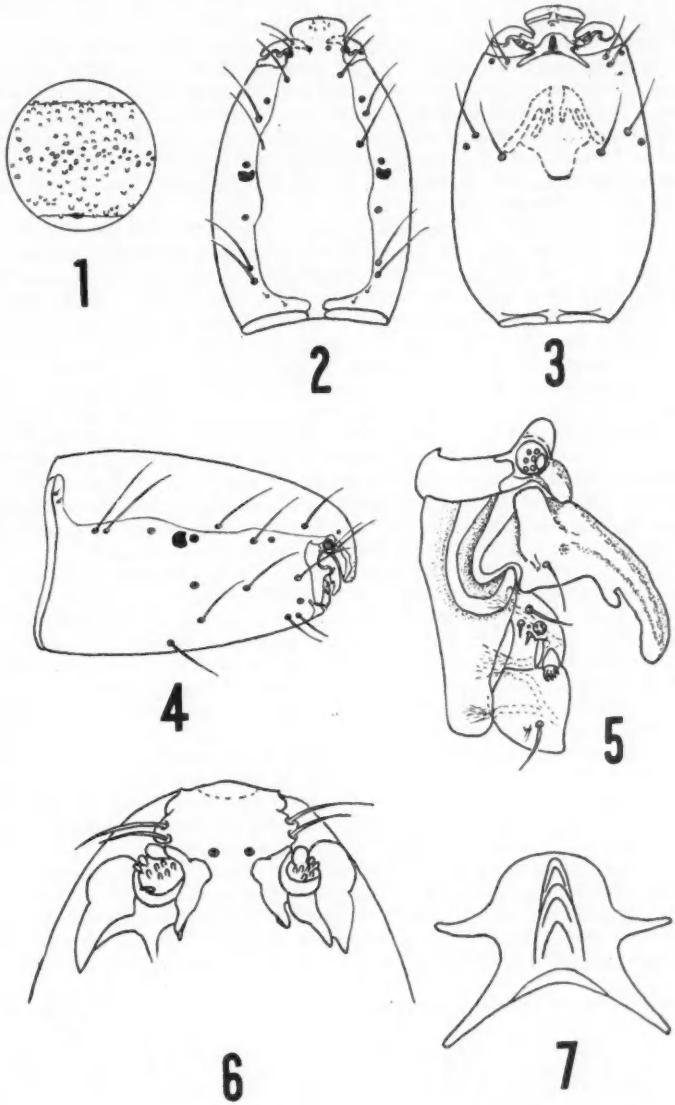
---

EXPLANATION OF PLATE I

Culicoides tristriatulus Hoffman. FIG. 1. Sculpturing on the chorion of the egg. FIG. 2. Dorsal aspect of the head of a mature larva. FIG. 3. Ventral aspect of the head of a mature larva; note broad lateral expansions of the floor of the ventral plate of the hypopharynx. FIG. 4. Lateral aspect of a head of a mature larva. FIG. 5. Right mandible and maxilla of a mature larva; note antenna directly above dorsal articulation of mandible. FIG. 6. Dorsal aspect of the cephalic portion of a head of a mature larva illustrating antennae, the two pairs of setae in front of the antennae and the fifth pair of cephalic sensory pits. FIG. 7. The labial plate of a mature larva.

Immature Culicoides tristriatulus
Roger G. Williams

PLATE I



thumb-like process half way along the length of the inner margin and rather prominent points of articulation. The thumb-like process, when observed from the ventral surface, can be seen to be composed of two processes or sections. The inner section is somewhat shorter and blunter than the outer. A single seta lies near the ventral articulation. No setae were reported on the mandibles of the other species but Tokunaga (1937) found two sensory pits in this approximate location on the mandibles of *C. circumscriptus*. On the mandibles of some specimens of *C. tristriatulus* a "ghost" of a single pit could be seen cephalad to the seta.

The maxilla, like the mandible, may be specific in structure. That of *C. tristriatulus* (fig. 5) consists of two lobes each of which is supported on its ental surface by a highly sclerotized thickening which has two widely divergent, subequal branches. The ectal surface of the dorsal lobe bears most of the appendages of the organ, all of which are directed ventrad. On the cephloventral margin is a short broad stalk crowned by four anteriorly curved spines. Dorsocaudad to this structure is a very large spine on a short tubercle which may be homologous to the palpus of authors, although this structure appears to be but a single segment in this species whereas a two-segmented palpus is described for most species. Dorsal to this spine is a tubercle bearing three or more small spines and caudal to this structure are three or four spines of various lengths. Near the dorsal articulation is a medium sized seta. The ventral lobe bears near its ventral margin a medium sized seta and a minute tubercle with one or two setae arising from it.

The labrum or clypeolabrum (fig. 8) which lies more or less in a verticle position, bears on the ectal surface on each side of the midline at least five small setae arising from short tubercles. The most ventral pair is the largest and the most dorsal pair next in size. Laterad is a group of three small paddle-like papillae on each side. At the end of the labrum is located a slightly arched row of five to seven spade-like teeth which are not highly sclerotized and in some larvae were most difficult to see. Caudal to them is a somewhat more heavily sclerotized arch which bears at its crest on the midline a triangular patch of rather obscure, minute teeth. On each arm of the arch are usually found three teeth, more rarely four or five. The two teeth nearest the triangular patch are more bluntly rounded and close together while the third tooth is set apart and is somewhat sharper.

The anterior margin of the labial plate (fig. 7) is rather transparent while its lateral and center portions are heavily sclerotized. The latter area appears to be composed of five cone-shaped structures directed forward and arranged in a stair-step fashion. The third and fifth "steps" are the longest. The first and second arise from the base of

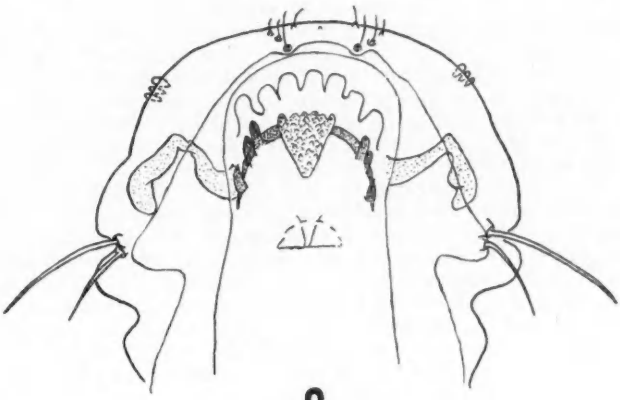
---

EXPLANATION OF PLATE II

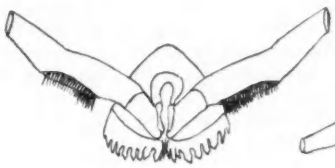
Mature larva of *Culicoides tristriatulus* Hoffman. FIG. 8. Ectal surface of the tip of the labrum. FIG. 9. Dorsal aspect of the dorsal plate of the hypopharynx. Fig. 10. Ventral aspect of the dorsal plate of the hypopharynx. FIG. 11. A single anal gill. FIG. 12. The caudal aspect of the ninth abdominal segment illustrating the arrangement of the setae about the anal opening.

Immature Culicoides tristriatulus
Roger W. Williams

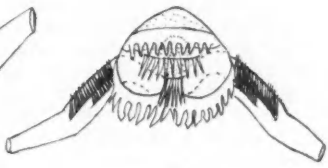
PLATE II



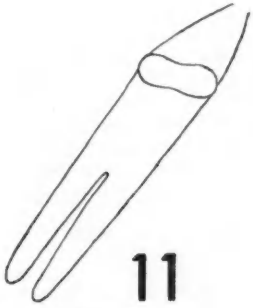
8



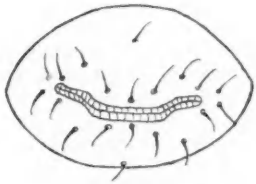
9



10



11



12

the third and the fourth from the base of the fifth. No lateral teeth are evident as indicated in some of the other species.

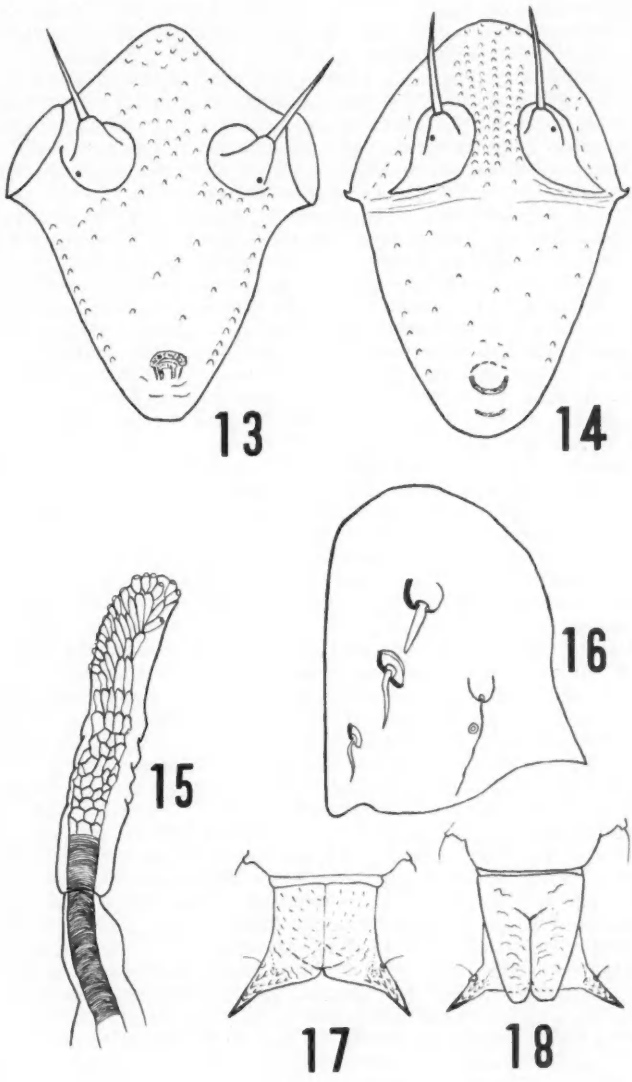
Most investigators agree that the hypopharyngeal region affords an important means of larval identification. The sclerotized arms of the dorsal plate of the hypopharynx of *C. tristriatulus* (figs. 9 and 10) each bear two rows of needle-like spines on the posterior margin. The dorsal row consists of 18 to 20 long slender spines of about equal length while the ventral row is approximately half as long with the spines becoming progressively shorter as the row progresses outward from the base. *C. obsoletus* illustrated by Hill (1947) is the only one of the several other species mentioned which has any spines in this location. In this species the dorsal row is composed of coarser teeth than the ventral row, the two rows apparently are of nearly equal length and the spines apparently proceed to the base of these arms, whereas in *C. tristriatulus* they appear to end a short distance from the base. The dorsal plate itself is composed of two caudal pieces with overlapping mesal edges. Each of these pieces have on their caudal border a row of 8 or 9 broad pointed teeth. The ventral surface of this plate (fig. 10) presents three more rows of teeth. The posterior row lies on the midline and is composed of 5 to 8 slender needle-like teeth directed caudally. The middle row consists of from 6 to 10 caudally directed needle-like spines, while the cephalic row, arising from a broad ridge, is composed of from 9 to 14 short, broad teeth. There is frequently a short spine on each end of the row and one or two smaller spines wedged between the larger ones in the row. The ventral plate of the hypopharynx appears much as described for *C. circumscriptus* by Tokunaga (1937) with some modification in the shape of the lateral rods and the two smaller pairs of central rods. The floor of the plate (fig. 3) has large lateral expansions which are not evident in Tokunaga's illustration of *C. circumscriptus*.

The setae of the thoracic and abdominal segments are all small and inconspicuous but appear to be more numerous on the thoracic segments than on the first eight abdominal segments. The ninth abdominal segment bears 10 pairs of setae arranged in a definite pattern around the anal opening as indicated in fig. 12. The number and possibly the arrangement of these setae appear to vary from species to species. Four retractile anal gills are present. These are usually retracted in preserved material and are almost impossible to see without teasing them out. Each gill is about 135 μ in length by 39 μ in width and each is deeply cleft (fig. 11), thus differing from those of some other species which have been illustrated, which appear to be rather shallowly cleft but agreeing in this respect with *C. kiefferi* Patton (Patton, 1915). The cleft in *C. tristriatulus* is about 93 μ in length. The gill tips are broadly rounded as opposed to those of several species illustrated

---

EXPLANATION OF PLATE III

Pupa of *Culicoides tristriatulus* Hoffman. FIG. 13. Operculum from the head capsule of a female. FIG. 14. Operculum from the head capsule of a male. FIG. 15. Respiratory trumpet. FIG. 16. The arrangement of the dorsal tubercles on the cephalic half of the mesothorax (only the right half is illustrated). FIG. 17. Ventral aspect of the terminal segment of the female abdomen. FIG. 18. Ventral aspect of the terminal segment of the male abdomen.


13
14
15
16
17
18

which appear to be sharply pointed and bulbous at the base. However, this appearance of the gills of *C. tristriatulus* may have been caused by standing overnight in trisodium phosphate prior to manipulating them through the anal opening.

Pupa.—The pupae of *C. tristriatulus* vary in length from 3.2 to 3.9 mm., averaging about 3.6 mm. Coloration is variable from yellow-brown to nearly black, depending upon the sex and the stage of pupal development. Sexual dimorphism is evident. As with all *Culicoides* and many other genera of Diptera, the male pupae may be readily distinguished from the female by the terminal cases on the ventral surface of the last abdominal segment which carry the developing forceps of the male hypopygium (fig. 18). The male abdomen tends to be somewhat longer and narrower than that of the female. It is also darker in color with a lighter band at the apical margin of the segments. These differences are not as evident between the exuviae as they are between the pupae themselves. The opercula of the head capsules of the sexes are different in several respects. That of the female (fig. 13) is broad in the "shoulders" and presents an appearance at this point similar to that of the arm holes of a sleeveless sweater, although no openings actually exist. Prominent in this area are two large tubercles each possessing a sensory pit at the base and terminating in a single large spine. Near the posterior angle of the operculum is a small sclerotized area of a rather indefinite design which may vary considerably in shape in different specimens. Blunt, squamose spines are scattered over the surface, being somewhat more numerous at the margins and behind and between the tubercles. The male operculum (fig. 14) lacks the obvious "arm hole" appearance, is narrower at this point with small upcurved hooks on the angles and the tubercles may be somewhat closer together. The scattered squamose spines are crowded together in straight rows between and in front of the tubercles.

The significance of the respiratory trumpet for delineating species has been emphasized by many authors. That of *C. tristriatulus* (fig. 15) is relatively straight and slightly flared at the distal end, measuring 230 to 270 μ in length, averaging 254 μ. The trumpet sits on a pedicle which is 65 μ in length which in turn arises from a tubercle on the thorax. Both the pedicle and the basal half of the trumpet are pale while the apical portion of the trumpet is dark brown to black in color. The tracheal trunk appears normal for a short distance into the base of the trumpet where it then gives rise to several rows in a number of layers of fish-scale-like "cells" which are lined with taenidia. These "cells" are angular at the basal extremity of the trumpet but become elongate and possess smoothly rounded ends as they approach the distal end where they terminate in a fan-like group of short spiracular openings set about the periphery. These openings appear to vary in number from 14 to 20 with 16 occurring most frequently. At about the point where the tracheal trunk gives rise to the scale-like appearance the external wall becomes somewhat roughened and wrinkled creating an effect of slight pseudo-segmentation throughout the center portion of the trumpet. There are no scales on the trumpet and no spiracular openings other than those at the distal extremity.

The cephalic, thoracic, and abdominal regions bear setigenous

tubercles. The terminology used for these throughout this discussion will follow that used by Carter *et al.* (1920) and Hill (1947). The anterior-marginal tubercles, the pair arising from the operculum, have been discussed. The anterior-dorsal tubercles which arise on the upper margin of the eyes of the imago are smaller and bear two setae, the lateral one being longer and stouter. These bristles are less than half the length of the respiratory trumpets. The dorsolateral tubercles situated laterad to the base of the respiratory trumpets, are smaller and each is provided with a medium sized and a minute seta, the latter being on the lateroventral surface. Rather inconspicuous rounded humps situated near the lower margins of the eyes, the ventrolateral tubercles, each have two setae of different lengths arising from their apex. The ventromedian tubercles near the midventral line of the cephalic area are small and inconspicuous and bear two delicate setae. These tubercles and setae in the cephalic area are very similar to those described by Carter *et al* (1920) for *C. accraensis* but differ in some respects from those of *C. impunctatus* as described by Hill (1947).

The position and number of dorsal tubercles over the mesothorax of the enclosed insect and the structure and shape of their attached setae apparently vary from species to species. *C. tristriatulus* possesses four pairs of dorsal tubercles arranged as indicated in fig. 16 (only one side is illustrated) and all lying in the anterior portion. The anterior pair of tubercles is large and each tubercle bears a broad spine-like seta. The two pairs of tubercles mesocaudad are progressively smaller and the seta which arises from each is much more narrow than those of the anterior pair. The fourth pair of tubercles, from each member of which a long slender hair arises, lies laterad and slightly caudad to the middle member of the three pairs just mentioned. Caudad to this fourth pair of tubercles is a pair of sensory pits. A second pair of isolated pits lies laterocaudad to the first in the posterior half of the mesothorax. The pair of posterior-dorsal tubercles appear to be wanting in *C. tristriatulus*, however, there is located on the mesothorax near the position where this pair of tubercles is evident in other species a pair of grouped sensory pits. Each member of the pair consists of three pits arranged in a triangle. Directly caudad to them lies a single pair of sensory pits on the first abdominal segment.

The abdomen consists of nine well marked segments. The first is slightly shorter than the others, the last elongate, and the seven intermediate segments sub-equal in length. The setigenous tubercles of the first, second, and eighth segments are reduced in number. Segments 3 to 7 have seven dorsal pairs of setigenous tubercles of which there are two in the cephalic row and five in the caudal, four lateral pairs consisting of one in the anterior half and three in the posterior half, and three ventral pairs in a row on the caudal half. The location of these tubercles is approximately the same as those described for *C. circumscriptus* by Tokunaga (1937), *C. impunctatus* by Hill (1947) and *C. accraensis* by Carter et al (1920). Sensory pits are present at least on some segments of the abdomen, however, it is impossible to see them on the pupae and very difficult to determine their exact location on the exuviae. The terminal segment bears two dorsally directed, curved, divergent, lateral processes with sharply pointed and highly sclerotized

tips, which are considered by Carter *et al.* (1920) to be highly developed lateral tubercles (figs. 17 and 18). The angle at which these caudal processes lie has been considered by many taxonomists of diagnostic importance. Tokunaga (1937) states that these spines are never at right angles to the body axis and that this is characteristic of the genus. He then gives an exception to this rule, that being *C. dovei* as illustrated by Dove *et al.* (1932). After examining numerous pupae of *C. triastriatulus* is was evident that these spines may be movable and may, therefore, actually be spurs since the angle at which they became fixed at death varied anywhere from right angles to the body axis to approximately 40° with the axis, thus permitting a range of movement of about 50°. It can be said of *C. tristriatulus* that the angle at which these terminal processes lie is of no taxonomic value. On the ventral surface of these spur-like structures are a number of sharply pointed, squamous, scales. Also on each of these structures is a pair of pits, one of the pair lying on the dorsal surface and the other on the lateroventral surface. From the center of each pit arises a thin, delicate seta which is exceedingly narrow in diameter in comparison to the pit from which it arises.

LITERATURE CITED

Buckley, J. J. C. 1934. On the development, in *Culicoides furens* Poey, of *Filaria* (*Mansonella*) *ozzardi* Manson, 1897. Jl. Helminth., 12: 99–118.

1938. On *Culicoides* as a vector of *Onchocerca gibsoni* (Cleland and Johnston, 1910). Ibid., 16: 121–158.

Carter, H. F., Ingram, A., and **Macfie, J. W. S.** 1920. Observations on the ceratopogonine midges of the Gold Coast with descriptions of new species. Pt. II. Ann. Trop. Med. & Parasit., 14: 211–274.

Dove, W. E., Hall, D. G., and **Hull, J. B.** 1932. The salt marsh sand fly problem (*Culicoides*). Ann. Ent. Soc. Amer., 25: 505–527.

Fox, I. 1942. The respiratory trumpet and anal segment of the pupae of some species of *Culicoides* (Diptera: Ceratopogonidae). Puerto Rico Jl. of Pub. Health. & Trop. Med., 17: 412–425.

Hill, Marjorie A. 1947. The life-cycle and habits of *Culicoides impunctatus* Goetghebuer and *C. obsoletus* Meigen, together with some observations on the life-cycle of *C. odibilis* Austen, *C. pallidicornis* Kieffer, *C. cubitalis* Edwards and *C. chiopterus* Meigen. Ann. Trop. Med. & Parasit., 41 (1): 211–274.

Painter, R. H. 1926. The biology, immature stages, and control of the sandflies (biting Ceratopogoninae) at Puerto Castilla, Honduras. 15th Rep. Med. Dep. United Fruit Co., 245–262.

Parker, A. H. 1950. Studies on the eggs of certain biting midges (*Culicoides* Latreille) occurring in Scotland. Proc. Roy. Ent. Soc. London, Series A 25, Parts 4–6: 43–52.

Patton, W. S. 1913. *Culicoides kiefferi*, n. sp.: a new Indian blood-sucking midge. Ind. Jl. Med. Res., 1: 336–337.

Sharp, N. A. D. 1928. *Filaria perstans:* its development in *Culicoides austeni*. Trans. Roy. Soc. Trop. ; Med. Hyg., 21 (5): 371–396.

Steward, J. S. 1933. *Onchocerca cervicalis* (Railliet & Henry 1910) and its development in *Culicoides nubeculosus* Mg. Cambridge Univ. Institute of Animal Pathology, 3rd Rept., 272–284.

Tokunaga, M. 1937. Sand flies (Ceratopogonidae, Diptera) from Japan. Tenthredo, 1 (3): 233–338.

Williams, R. W. 1951. Observations on the Bionomics of *Culicoides tristriatulus* Hoffman with notes on *C. alaskensis* Wirth and other species at Valdez, Alaska, Summer 1949 (Diptera, Heleidae). Ann. Ent. Soc. Amer., 44(2): 173–183.

DESCRIPTIONS AND NOTES ON NEOTROPICAL TABANIDAE

G. B. FAIRCHILD
Gorgas Memorial Laboratory,
Panama, R. P.

The material here discussed has accumulated from various sources during the past four years.[1] It consists of a number of apparently undescribed forms from several parts of the Neotropics together with new information regarding some described species and new distribution records for the Republic of Panama. The eight species added to the fauna of Panama bring the total to 106 species now definitely known from this area. (For synonymy of species previously discussed by me see list of references at the end of this paper.) Types of new species will be deposited in the Museum of Comparative Zoology, Cambridge, Mass.

Fidena schildi (Hine)

As was considered probable, (Fairchild, 1941, Ann. Ent. Soc. Amer., 34 (3): 644) this species has now been taken in Panama. My colleague, Dr. Galindo, secured a single specimen, together with two of *F. pyrausta* (O.S.) at an isolated Indian village on the Rio Caña, Bocas del Toro Province, 9 July, 1949. They were attacking domestic pigs at 6 A. M. under a shed where Dr. Galindo had taken shelter from heavy rain.

Fidena pyrausta (O. S.)

Two females taken with *F. schildi* and four additional females from Palo Santo, Chiriqui Province, 15 and 22 June and 14 July, 1950. These latter were taken by Dr. Galindo's mosquito catchers while attempting to bite them. One of these speciemens has the abdominal hairs pale straw colored, while in the others it is rufous orange. All but one have the fourth to last tergites clothed with orange or yellow hair. This last agrees with my original specimens in having the fourth tergite black haired. It also differs from the others in having the squamulae at the base of the wing fringed with silvery white hairs, (black in the other specimens) and in the first posterior cell being closed and petiolate (open in all the others). There are also traces of white hairs middorsally on tergites III and IV in this specimen. Structurally I can perceive no differences, and believe this to be but an extreme variant. I also have a single specimen from Ecuador, Luis Leon coll., which agrees perfectly with this last specimen.

[1]Most of the Panama material discussed herein was collected by my colleagues, Dr. Pedro Galindo and Dr. Harold Trapido, or by the mosquito catchers working on a project under the direction of Drs. Galindo, Trapido and Col. S. J. Carpenter, M.S.C. Unless otherwise noted, the Panama material was collected by this group. Cost of publication is paid by the Gorgas Memorial Institute.

Fidena columbiensis Kröber

Melpia columbiensis Kröber 1930, Mitt. Zool. Mus. Hamburg, 44: 177 (♀, Upper Condosa, 22. XLI., Condota, 5).
Fidena columbiensis Kröber 1934, Rev. Ent. 4(2): 247. Bequaert and Rengifo, 1946, Psyche, 53(3–4): 61.

Five females from Palenque, near the mouth of the Rio Cuango, Colon Province, Panama, 12 Sept., 1949, R. Hartmann coll. This locality is on the Caribbean coast, about 60 miles east of Colon. As indicated by Bequaert and Rengifo, the type locality was probably the Rio Condoto, Choco, Colombia, the part of Colombia adjoining Panama on the east.

The specimens have the following characters. Length 14–17 mm., wing 13–14 mm. Frons about three times as high as wide, slightly narrowed at vertex, dark-brown pollinose, black haired. Eyes densely short brown pubescent. Face quite produced, snoutlike, brown pollinose above, shiny on the sides. A tuft of black hairs below the antennae extending to the eye margin. Beard creamy white to nearly snow white. Antennae dark brown, the third segment of eight divisions, of which the first three are largest and seemingly less freely articulated. Palpi dark brown, slender, acute, the terminal segment about equalling the last six segments of antennae. Outer surface of palpi flat, brown pollinose, with a marginal fringe and the slender apex black setose. Proboscis 7–9 mm. long, the labellae sclerotized and slender.

Mesonotum dark brown, dark-brown pollinose, sparsely black haired, without marked stripes. In some specimens there are a pair of small pale-pollinose patches before the scutellum. Scutellum concolorous, its hind margin paler. Margins of mesonotum with sparse grey hairs anteriorly, dense black hairs laterally, and mixed yellowish and black hairs between wing roots and scutellum. Pleura and sternum pale greyish white, the former densely creamy to white haired, the latter sparsely dark haired. Legs wholly orange yellow, orange haired, except the coxae, and especially the fore coxae, which bear dense long dark hairs. Wings uniformly smoky, without blackish bases. First posterior cell open but more or less coarctate in four specimens, closed at the margin in the fifth. Abdomen dark brown, densely black haired, but with small median yellowish hair tufts on second to sixth tergites, sometimes also on the first. Extreme sides of tergites creamy haired. Sternites pale, whitish pollinose and pale haired.

The species may be easily distinguished from others of the genus in Panama by its wholly pale legs, and the contrasting colors, whitish below and nearly black above. The structural characters of the head region are rather uniform in this genus, and are not very suitable for specific differentiation. *Fidena auribarba* End. and its var. *albibarba* End. (1924), also from Colombia, seems exceedingly close from the descriptions, but Kröber (1930), who has seen the types, maintains its distinctness.

Fidena bicolor Kröber

1931, Zool. Anz. 95(1–2): 36–37 (♂, Higuito, San Mateo, Costa Rica); 1934, Rev. Ent. 4(2): 246.

A single female, Quepos, Damas, Costa Rica, 4 Oct., 1950, sent to me by the collector, Mr. J. R. Kuppers of the United Fruit Company.

This specimen agrees fairly well with the original description, except that the abdomen is wholly yellow haired. The male described by Kröber is stated to have had the abdominal tergites broadly margined with yellow hairs, the species being compared with *auricincta* Lutz and Neiva. I believe, however, that the differences noted are merely sexual.

The specimen at hand may be designated as *neoallotype* and has the following characters: frons as in *Fidena isthmiae* Fchld. (1941), the fronto-clypeus grey pollinose, antennae black. Palpi as in *isthmiae*, though relatively shorter than in most specimens of that species. Beard pale yellowish brown. Legs wholly black, short haired. Mesonotum, pleura and sternum dark brown, black haired, with a tuft of yellowish brown hairs before the wing bases, and the hairs on the squamulae yellowish brown. Wings yellowish hyaline, black at extreme base, the first posterior cell closed and petiolate. Abdomen with first segment black and black haired, the remaining segments dirty yellowish horn-colored, clothed both above and below with rather short appressed golden yellow hairs.

The species may be distinguished from all others of similar coloration known to me by the combination of wholly black legs and unusually narrow frons. It is structurally indistinguishable from *F. isthmiae*, but the strikingly colored abdomen precludes the merging of the two forms until evidence of intergradation appears. *F. isthmiae* itself is proving somewhat variable with the accumulation of more material. The hairs on the squamulae may be either blackish brown or silvery white, the antennal flagellum varies from black to reddish brown, and the shape of the palpi is hardly the same in any two specimens.

Esenbeckia mejiae Fairchild

1942, Ann. Ent. Soc. Amer., 35 (2), p. 198, pl. 1, fig. 8. James, 1950, Pan-Pac. Ent., 26 (2): 87–88, fig. 1 (♂; Agua Amarilla, Honduras).

Three specimens (1 ♀, Choluteca, Honduras, Oct. 1945; 2 ♀, Boqueron, Tegucigalpa, Honduras, 26 Oct. 1942) differ sufficiently from the type to have been considered as specifically distinct. However, considering that they come from practically the same locality and were taken at the same time of year, I hesitate to consider them more than variants. They differ from the type in being more orange in ground color, in having the coxae and bases of femora wholly orange haired, in having the palpi more slender and drawn out, and in the frontal callus being mostly covered with pollen. This last feature is hardly important, as the type may have had this area rubbed, and the three specimens at hand show various degrees of denudation. The palpi also vary somewhat, and since they are quite thin, it is possible that shrinkage may have caused the edges to curl slightly in the present specimens, thus giving them a more slender aspect. The strikingly inflated and shiny face, long terminal annulus of the antennae and other characters appear to be the same.

Esenbeckia yepocapa sp. nov.

Female.—Length 17 mm., wing 17 mm. Eyes bare. Frons about 4 times as high as wide, orange brown pollinose, including the slightly raised ridge-like callus and vertical tubercle. Subcallus pollinose;

fronto-clypeus and genae thinly brown pollinose, the tentorial pits deep, close to eye margin, and with a fringe of long yellow hairs along eye margin. Beard whitish yellow. Antennae with first two segments brown, black haired, third segment bright orange brown, of eight visible annuli, of which the first is the largest and is partially fused to the next three, the terminal four being more slender, while the last is long and spike-like. Palpi dark mahogany brown, black haired, long and slender with attenuated tips, the middle section of the outer side being somewhat hollowed out or funnel-shaped and free of hairs. Face not snout-like, proboscis about equalling head height, the theca and labella well sclerotized, though the latter not immovably fused.

Thorax and scutellum mahogany brown, subshiny, thinly greyish brown pollinose and clothed with fine dark hairs. Pleura and sternum more densely grey pollinose and clothed with long pale grey hairs. Legs orange brown, the coxae and femora darker. Coxae clothed with long black and grey hairs, femora with shorter black hairs, the tibiae and tarsi with very short golden hairs. Wing yellowish hyaline, more intense in costal cell and along fore border. Area basal to arculus, squamae, and extreme bases of basal cells deep black. First posterior cell closed and petiolate; upper branch of third vein with a long appendix. Subepaulet bare, costa and first vein setose above, subcosta bare. Abdomen shiny mahogany brown above, black haired except the lateral angles of tergites I to VI, which bear tufts of creamy white hairs. Venter shining brown, dark haired, except a narrow row of pale hairs on the hind margins of all sternites, widened into a small tuft on the posterior angles.

Male.—Length 15–19 mm., wing 15–18 mm. Eyes bare, holoptic, the facets essentially of equal size, though those on the disk appear very slightly larger than those along the lower margin. Vertical tubercle prominent, rising above eye level, pollinose in front, hirsute behind with three well developed ocelli. Frontal triangle brownish pollinose. Antennae as in female, but more slender. Palpi slender, shorter than in female and rather blunt pointed. The hollowing evident in the female is not so pronounced, the outer surface of the palp being nearly flat and free from hairs in the middle. In all other respects the male is like the female, though somewhat more densely haired.

Holotype female, *allotype* male and 31 *paratype* males, Yepocapa, Chimaltenango, Guatemala, November 19, 22, 24 and 27, 1944. The specimens were taken hovering over the roads through coffee plantations, resting on vegetation along the roads, or on the flowers of a large species of Compositae. The single female has the beard thickly clogged with pollen grains. Although searched for, no females were seen attacking animals or man.

The species appears to be very closely related to *Esenbeckia wiedemanni* Bellardi. It differs in having a somewhat broader frons and more acutely pointed palpi in the female and in color characters. In *wiedemanni* the legs are mainly blackish, the hind tibiae especially being black and black haired, while in *yepocapa* the tibiae are bright orange yellow and orange haired. The abdomen of *wiedemanni* has the first segment pale pruinose and pale haired, while the remaining segments are without pruinosity and with sparse and short pale hairs. In

yepocapa the first segment is nearly as shiny as the rest of the abdomen and bears dark hairs. The remaining abdominal tergites are sparsely black haired. The single available female of *yepocapa* has been compared with a series of females of *wiedemanni* from Chiapas, Mexico. Further material may show that these characters intergrade, and that *yepocapa* is but a southern race of *wiedemanni*.

Wiedemanni is included by Enderlein (1925) and Kröber (1934) in the former's genus *Ricardoa*, based on species with palpi less than half length of proboscis. Both Bellardi's description and figure, however, show the palpi to be long. In the case of *E. saussurei* Bell., the matter is not so clear. Bellardi states that the palpi are long and falcate, though his figure shows them to be considerably less than half the length of the proboscis. Material which Dr. Bequaert and I have called *saussurei* is probably not that species, as the palpi are very short and hollowed-out or funnel-shaped on the outer aspect. Our specimens also lack the light dorsal stripes on the thorax mentioned and figured by Bellardi.

The status of *Ricardoa* Enderlein will need eventual clarification. Although I do not have before me as ample material as would be desirable, it might be well to point out that the character of the length of the female palpus, used to separate *Esenbeckia* and *Ricardoa*, is of dubious utility, first, because the proboscis, or at least the labium, is somewhat extensile, and so varies in apparent length, and second, a number of species show palpi slightly less than half as long as the proboscis. *E. incisuralis* Say has them considerably less than half as long, *E. prasiniventris* Macq. has them a little more than half as long, and *E. translucens* Macq. has them nearly two-thirds as long. A specimen which Dr. Bequaert and I believe to be *E. planiventris* Macq. 1850 has very short palpi, hardly one-fourth the length of the proboscis. It is placed by Kröber, with a query, as a synonym of *E. saussurei* Bell. in the genus *Ricardoa*. Since the original description and figure of *saussurei* both indicate rather long palpi, we believe the two are distinct species.

In regard to *Proboscoideus* Philip I have specimens of two species which belong certainly to the group. One was determined as *Esenbeckia ferruginea* var. *nigrovillosa* Kröb. by Dr. G. M. de Oliveira Castro, as previously noted by me (Fairchild, 1942, p. 197). However, Dr. C. B. Philip informs me that the type of *nigrovillosa*, examined for him by Dr. Max Beier in the Vienna Museum, has a perfectly normal proboscis. My material is very close to *Proboscoides fairchildi* Phil., but has pale haired palpi and largely dark haired abdomen and legs. It is from Goyaz, Brasil, and may well be a race of *fairchildi*, though comparison with the types of the latter will be necessary to settle its status. *Esenbeckia inframaculata* Lutz also has the proboscis of similar structure and should be placed in this group.

Dichelacera melanosoma Hine

Figs. 4, 4a, 4b

1920, Ohio J. Sci. 20 (8): 316, fig. 1 (♀; Higuito, San Mateo, Costa Rica); 1925, Occ. Pap. Mus. Zool. Univ. Michigan, no. 162, p. 35 (in key only).

Catachlorops melanosoma Kröber 1931, An. Mus. Nat. Hungarici, 17: 344–345, fig. 11 (2 ♀, Higuito, San Mateo, Costa Rica); 1934, Rev. Ent., 4 (2): 273. Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22: 153 (in key only).

A single somewhat battered specimen from Progreso, Chiriqui Prov., Panama, 13 July, 1950, agrees perfectly with Hine's description. The nearly black wings and body led Kröber to place it in *Catachlorops*, but in my opinion it belongs in *Dichelacera* s.s. In Barretto's (1946) recent division of the genus *Dichelacera*, it would run to *Rhamphis* End., except that the antennae are long and slender, with a dorsal spine reaching the first annulus.

Dichelacera marginata Macq.

This species is proving to be very variable in color. A series of specimens from Ft. Sherman, C. Z., and Piña, Colon Province, Panama, Dec. 1948, are quite dark, the interalar dark band much wider than the prescutellar pale band and the pollinosity and vestiture of hairs tending to be greyish. A further series from Paraiso, C. Z., Nov.-Dec. 1948, and Sept.-Oct. 1950, are similar, though on the average more yellowish. Both series show the abdominal pale bands considerably less than half the width of the tergites and the wing picture quite dilute, hardly more than a faint narrow dusky band from apices of submarginal cells to apex of anal cell. A series from Candelaria Hydrographic Station, upper Rio Pequeni, Panama, is very much lighter and more yellow. The interalar dark band is narrower or about as wide as the prescutellar pale band, the abdominal pale bands are at least half as wide as the segments and may be wider. The legs are less infuscated, but the wing picture darker. A specimen from Progreso, Chiriqui, Panama, 7 Sept. 1950, appears also to belong to the yellow form, though it is rather rubbed. Finally, a specimen from El Real, Darien, Panama, 11 July 1950, is dusky brownish all over, with no trace of yellow hairs whatever. All the above are structurally alike, and I believe do not warrant names.

Dichelacera regina Fairchild 1940

With the taking of adequate series of this hitherto rare species, some puzzling variation has shown up. Twenty-five specimens from Sta. Fe, Veraguas Prov., 24 May to 11 Aug., 1950, 2 specimens from Progreso, Chiriqui Prov., 28 July, 1950, and 1 from Cerro Campana, Panama Prov., 10 Aug., 1950, agree closely with the original material from El Valle, Cocle Province. A series of 17 specimens from Cerro Campana, 12 June to 5 September, 1950, 4 specimens from Candelaria Hydrographic Station, upper Rio Pequeni, Panama Province, and 6 specimens from La Victoria, Cerro Jefe, Panama Province, June and August, 1950, average smaller in size, with broader frons, shorter antennal tooth and less even proximal border of the dark fascia of the wing. The great majority also have at least some yellow hairs on the fifth abdominal tergite and often a broad yellow-haired band.

All of the above localities are in areas of heavy forest and, with the exception of Progreso and Candelaria, at elevations of about 2000 ft. Cerro Campana is a rather isolated group of hills about 40 miles west of the Canal Zone and separated from El Valle, a similar isolated massif, by a broad valley about 10 miles across. Sta. Fe and Progreso are much further west, while La Victoria and Candelaria are about 20 miles east of the Canal Zone. The two forms might be treated as geographical races, an Eastern and Western, but the presence of both

forms on Cerro Campana and our lack of material from other localities makes a decision seem unadvisable as yet.

Dichelacera (Dichelacera) rex sp. nov.

Figs. 1, 1a, 1b, 1c

Female.—Length 10–11 mm., wing 10.5–11 mm. Eye bare, in life green or yellowish bronze with a single median transverse dark-purple band; the upper, and to a less extent, the lower margins more or less purplish also, so that in some specimens the eye may be said to be purple with two very broad green bands. Frons dark-yellow pollinose, about four times as high as wide, slightly narrowed at vertex, the frontal callus black, as high or higher than wide, and prolonged above in a slender point. Vertical tubercle with vestiges of at least the anterior ocellus. Antennae and palpi as figured, the former dirty yellowish brown on first two and base of third segments, the remainder blackish. Palpi orange yellow, mostly black haired. Subcallus, fronto-clypeus and genae golden yellow pollinose, the last with a sparse yellow beard. Proboscis black, less than head height, the labella shiny.

Mesonotum black with two narrow deep-yellow-haired cross-bands. The area before the anterior cross-band is partially yellowish pollinose, but with mainly black hairs. The posterior yellow band is less than half as wide as the preceding dark band. Scutellum black. Pleura and sternum deep yellow pollinose, sparsely yellow haired. Legs yellow, except apices of fore tibiae and tarsi, apices of hind femora, hind tibiae and tarsi. Wings as figured, the clear areas quite yellow, the dark areas black. Abdomen yellowish brown in ground color, the first tergite yellow haired, the rest black haired, with broad yellow haired triangles on the second, third and fourth tergite. There are also patches of golden hairs on the sides of these tergites. Beneath the abdomen is dusky yellowish, sparsely yellow haired.

Holotype female and 5 female *paratypes*, Candelaria Hydrographic station, upper Rio Pequeni, Panama, 15–21 August, 1950; 5 female *paratypes*, Sta. Fe, Veraguas, Panama, 24 May, 28 July (2), 3 and 11 August, 1950; 2 female *paratypes* near Almirante, Bocas del Toro Prov., Panama, 16 May, 1951. One of the Sta. Fe specimens was taken 40 feet up in a tree at a mosquito catching station, the others at ground level.

This species was first thought to be but an extreme variant of *regina* Fchld. but there are too many constant characters separating the two. The frontal callus seems to be slightly higher, the median prolongation more prominent and the frons narrower. The palpi in *regina* are wholly yellow haired, while in *rex* they are extensively black haired. The yellow vestiture of *regina* is considerably lighter in tone than in the present species, and the anterior part of the mesonotum is wholly yellow and yellow haired. The black band of the thorax is consistently broader in *rex*. The abdominal pattern in *regina* consists of complete transverse bands, reduced to triangular median patches in *rex*. The dark wing markings in *rex* are more extensive, the distal fascia extending well proximal to the fork of the third vein whereas in *regina* this never occurs. The wing markings are also more intense in *rex*. The wing markings of *rex* are just like Hine's figure of *caloptera*, but the frons of

that species is broader, the abdomen with transverse bands, and the face shiny. In *rex* the face is rather thinly pollinose, subshiny in some specimens.

Dichelacera analis Hine

A single male from Candelaria Hydrographic Station, Upper Rio Pequeni, Panama, Aug. 14, 1950. The coloration and wing pattern are as in the female, and there is no difficulty in associating the sexes. The antennae are somewhat more slender than in the female, the palpi porrect and long haired. The eyes are holoptic, the area of large facets extensive, fully two-thirds total eye area, the two types of facets strongly differentiated and demarcated from each other. The large-faceted area is dark brown, the small-faceted area purple with a single green transverse stripe in life. There are sparse, short and fine hairs scattered over the area of large facets. A small vertical tubercle is present.

Dichelacera (Catachlorops) umbratus (Hine)

Figs. 2, 2a, 2b, 2c

Tabanus umbratus Hine 1920, Ohio J. Sci., 20 (6), p. 187 (♀, Higuito, San Mateo, Costa Rica).

Catachlorops umbratus Krōber 1934, Rev. Ent., 4 (2), p. 274 (species incerta sedis). Fairchild, 1948, Ann. Rep. Gorgas Mem. Lab., 1947, p. 30 (Sta. Fe, Veraguas, Panama). Barretto, 1946, An. Fac. Med. Univ. S. Paulo, 22, p. 153 (in key only).

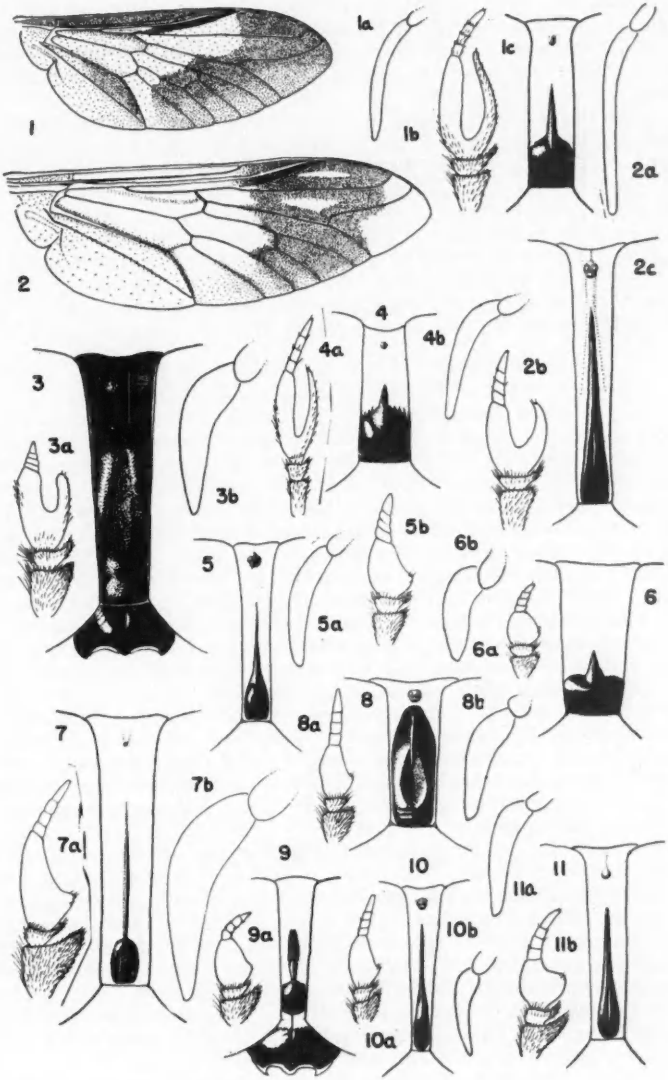
Eleven additional specimens show this species to be not uncommon at suitable localities. One specimen is from the Rio Chico Hydrographic Station on the upper Chagres river, 20 March, 1948, one from Utive, near Pacora, Panama Province, 27 Jan., 1949, three from Yellow Fever Station X, Chorcha, Chiriqui Prov., Panama, Jan. 11, 1951, and six from Yellow Fever stations in the vicinity of La Victoria, Cerro Jefe, Panama Province (1 ♀, Jan. 11; 2 ♀, Jan. 31, and 3 ♀, Feb. 1, all 1950). The last 9 specimens were taken attempting to bite men who were stationed at platforms from 37 to 50 feet up in trees catching forest mosquitoes.

The whole insect is dark chocolate brown with grey pollinosity. Dorsally the hairs are black, the thorax striped with grey. The fourth tergite bears a large median triangle of silvery white hairs, while the hind margin of the seventh tergite is also white haired. Ventrally the abdomen bears two broad longitudinal bands of dark hairs, otherwise the ventral parts are white haired. The legs are uniformly dark brown, the femora pale haired, the tibiae dark haired and the tarsi nearly black. The fore tibiae are obscurely to clearly bicolored. The frontal

---

EXPLANATION OF PLATE I

FIGS. 1, 1a, 1b, 1c. *D.* (*Dichelacera*) *rex* sp. nov., holotype. FIGS. 2, 2a, 2b, 2c. *D.* (*Catachlorops*) *umbratus* Hine. FIGS. 3, 3a, 3b. *Stibasoma theotaenia panamensis* Curran. FIGS. 4, 4a. 4b. *D.* (*Dichelacera*) *melanosoma* Hine. FIGS. 5, 5a, 5b. *Stenotabanus frondicolus* sp. nov., paratype. FIGS. 6, 6a, 6b. *Stenotabanus ananasi* sp. nov., holotype. FIGS. 7, 7a, 7b. *T.* (*Lophotabanus*) *fumomarginatus* Hine. FIGS. 8, 8a, 8b. *Leucotabanus leucogaster* sp. nov., holotype. FIGS. 9, 9a. *T.* (*Taeniotabanus*) *picicallosus* sp. nov., holotype. FIGS. 10, 10a, 10b. *Leucotabanus pauculus* sp. nov., holotype. FIGS. 11, 11a, 11b. *Leucotabanus weyrauchi* sp. nov., holotype.


1
1a
1b
1c
2
2a
2b
2c
3
3a
3b
4
4a
4b
5
5a
5b
6
6a
6b
7
7a
7b
8
8a
8b
9
9a
10
10a
10b
11
11a
11b

callus is ridge-like, mahogany brown. The vertical tubercle is small, pollinose, but with discernible vestiges of ocelli. The subcallus is pollinose, antennae wholly blackish brown, palpi white, sparsely black haired, thread-like. Proboscis as long as frons, the labella small and shiny. The eyes are bare, bright green in life. The subepaulet is without macrotrichiae.

This species is structurally closer to the subgenus *Psalidia* End. than to the more typical species of *Catachlorops*. The unicolorous green eyes would place the species in *Amphichlorops* were one to follow Baretto's classification. However, the color of the eyes is of dubious use when unsupported by structural characters. The species placed in these two genera by Barretto (1946, 1948) seem hardly distinguishable. In fact, I do not see how *Amphichlorops pechumani* Barr. (1948, p. 407) described from the female is to be separated from *Catachlorops zikani* Barr. (1946, p. 167) described from the male. Both were taken in the same general locality and in part at the same time of year.

Dichelacera (Psalidia) fulminea (Hine)

A series of over 50 specimens from various localities in Panama shows two rather distinct forms to be present. One of these, which agrees with Hine's *fulminea*, averages larger, (16–20 mm., aver. 18.4 mm.), is more deeply colored, the mesonotum and abdomen being deep rufous orange, almost coppery. The wings are very dark, practically black in some specimens, with subhyaline fenestrae in the marginal and first submarginal cells beyond the stigma and in the discal cell. The area below the stigma is yellowish subhyaline, and there are small paler areas in the fifth posterior cell and anal area. The eyes in life are bright green, slightly darker on the upper half, the dividing line between the two shades sharply marked. The other form is the one previously discussed by me (Fairchild, 1940, p. 693) and agrees with Hine's *festivus* and Enderlein's *ocellatus*. It averages smaller (12–16 mm., aver. 15.2 mm.) and is more yellow and lighter in tone throughout. The wings are much lighter, more yellowish hyaline basally and the apical blackish area contrasts more strongly with the basal area. The extent of the hyaline fenestrae in the marginal and first submarginal cells varies a good deal in both series, but on the average is about the same in both. The eyes of this form, in the few specimens seen alive, are uniformly bright green.

Although very different appearing, I can find no structural differences between the two. Both occur together at Santa Fe, Veraguas, at Cerro Campana, and at La Victoria, all areas of mountain forest at about 2000 ft. elevation. The types of both Hine's names were from Gatun, C. Z. The light form is the only one so far taken in other localities in Panama, and I have specimens also from San Luis, Peten, Guatemala, May, 1947, de Leon coll., and Fortin, Vera Cruz, Mexico, 20 May, 1947, W. G. Downs coll. These latter are rather paler and smaller than most Panama specimens, with the dark areas of the wing relatively reduced in area and intensity.

Between the two forms there are occasional intergrades. A single large dark specimen from Sta. Fe has wings precisely like the light form, while a small light-bodied specimen from the same locality has

wings as dark as some of the dark form specimens. Should it seem desirable to separate the forms nomenclatorially until their status is clarified, the name *ocellatus* End. is available and could be used in a varietal sense for the light specimens.

Stibasoma fulvohirtum (Wied.)

A series of 67 females from Progreso, Chiriqui (9, 16 and 23 June, 13, 28 July, 3, 10 and 17, August, 9, 16 and 30 November, 1950, and a single female from Cerro Campana, Panama Province, 12 June, 1950). The color of the vestiture varies somewhat, some specimens having the mesonotum wholly bright orange rufous haired, while in others there is considerable admixture of black, though none are quite as dark as the specimens from Trinidad mentioned by Knab (1913, Proc. U. S. Nat. Mus., 46: 412). The second and third tergites always bear a fringe of pale straw colored hairs, the remaining tergites have these hairs mixed with black ones to a greater or less extent, even to having practically no pale hairs.

Stibasoma theotaenia panamensis Curran

Figs. 3, 3a, 3b

A female specimen, Ft. Sherman, C. Z., 11 March, 1950, and another female, Arraijan, Panama, 4 Dec., 1950, enable me to add to the note on this species previously published (Fairchild, 1940, p. 685). Dr. C. B. Philip also reports (in litt.) a male from Barro Colorado Island, C. Z., 8 Mar., 1937, and a female from Chorrera, Panama, 19 Dec., 1944. The frons is similar to that of *apicimacula* Fchld., but a little broader and more convergent below. The frontal callus is hardly raised, and the median ridge is quite flat. There are dense black hairs on the upper part of the frons. The subcallus is quite protuberant, wholly shining black. Fronto-clypeus and genae, palpi and antennae black. The antennae are also similar to those of *apicimacula*, but thicker and heavier appearing, the dorsal spine just reaching the first annulus.

The thorax is jet black, black haired except for a small tuft of long silver white hairs just before the wing bases. The legs are jet black, black haired, except for the tarsi, which are brown and russet haired. There is also a small patch of long white hairs at the base of the hind tibiae on the outer surface. The abdomen is orange yellow in ground color, the first two tergites clothed with long lemon yellow hairs, the remainder with long copper or orange hairs. The third tergite bears also black hairs mixed with the coppery ones on the sides. Beneath the second sternite bears a patch of black hairs in the middle, coppery hairs on the hind margin and yellow hairs laterally, the remaining sternites being copper haired. The wings are deep black, with a narrow, diffuse subhyaline border from the first submarginal cell to the anal area. My specimens measure 16 and 12 mm. in length.

Stibasoma apicimacula Fairchild 1940

Three additional specimens of this species have come to hand in the last ten years (El Valle, Cocle Province, 16 June, 1946, H. Trapido coll. and Sta. Fe, Veraguas Province, 28 July and 4 August, 1950,

P. Galindo leg.). Both localities are in the mountains at an elevation of about 2000 ft. in heavy forest. The last two specimens were taken 40 feet up in a tree, at a mosquito catching station.

Triceratomyia mcintyrei Bequaert

1937, Rev. Ent., 7 (4): 350–353, 1 fig. (♀, Ecuador).

Additional material from Ecuador indicates that this species lacks spurs on the hind tibiae. Both Dr. Bequaert and I have re-examined the type, and find that it too lacks spurs, the comb on the tip of the tibiae resembling spurs as seen laterally. The species is quite similar in habitus and color to *Dasychela limbativena* End., but has bare eyes and even longer proboscis and palpi. *Triceratomyia* may also be compared with the African *Thaumastocera* Grunb. in regard to the antennae. In that genus, the antennae are also triramous in most cases, but the median prong may be reduced to a mere knob in some specimens. It is likely that the antennae of *Triceratomyia* have evolved from a biramous condition such as is found in many Neotropical Tabanids. *Thaumastocera* is placed by Enderlein in the *Dichelacerini*, I think correctly. It has bare subepaulets, and sclerotized labella much as in *Stibasoma*, although showing a number of specializations not found in any Neotropical members of the tribe.

Bolbodimyia bicolor (Bigot)

A single female taken in a horse-baited mosquito trap, Ft. Davis, C. Z., 22 Dec., 1948, C. M. Keenan leg. This specimen agrees structurally with material from Colombia and Brasil before me, and with the redescription of *B. erythrocephala* Bigot given by Kröber (1929). In color the specimen is more extensively orange red than other material I have seen, the whole frons and face, part of first and second antennal segments, palpi, whole venter, coxae and basal two-thirds to three-fourths of all femora are brilliant orange red. The hairs and pollinosity occurring on the orange areas are also orange. Elsewhere the insect is deep black. This differs from the description of *erythrocephala* in having the palpi, venter and femora red, as well as in lacking the white beard and white tarsi. Were it not for the latter two characters, I would unhesitatingly sink *erythrocephala* as a synonym of *bicolor*, as I have now seen specimens running the complete range from the present extensively orange specimen to those completely black. *B. desecta* End., *B. lateralis* Krob. and *B. nigra* Stone will all fall as synonyms of *bicolor*, and as Bequaert and Rengifo have indicated, the same is probably true for *erythrocephala*.

Stenotabanus jaculator Fairch.

A considerable series of additional specimens of this species enables me to describe the male and make some additions and corrections to my original description (1942, p. 309), which was drawn from old and rubbed material.

The eye in life is greenish bronze, with a single narrow and often faint median dark stripe. All tarsi and apices of fore tibiae are blackish, the legs otherwise being yellowish brown. The degree of infuscation

along the fore border and apex of wing varies somewhat, being quite intense in some specimens. The ground color of thorax and abdomen is usually dark olive, darker than stated in the original description. In perfectly preserved specimens the thorax is clothed with sparse brassy hairs. The vestiture of the abdomen consists of a fine silvery grey pollinosity on the first two segments, lacking on the remaining segments, and of rather sparse hairs, black for the most part, but with pale brassy hairs forming rather broad middorsal triangles on the first to fifth tergites, and patches on the posterolateral angles of all tergites. Beneath the sternites are thinly greyish pollinose and pale haired. The vestiture is sparse and easily rubbed off.

The male is somewhat paler and more hirsute than the female, but is easily associated on color characters. The eyes are entirely bare, holoptic, rather enlarged with a well demaracted area of enlarged facets occupying about one-half the total eye area. The small facets are bronzy green, the large facets brown. There is a well developed vertical tubercle with vestiges of at least the anterior ocellus. The antennae are more slender than in the female, and the subepaulet bears fewer macrotrichiae.

Neoallotype and *neoalloparatype*, males, La Victoria, Cerro Jefe, Panama Province, Panama, 2200 ft. elev., 20 April, 1949. Taken in a mosquito light trap. H. Trapido and P. Galindo colls. To be deposited in M. C. Z.

This little species has proven to be exceedingly abundant at this locality. A series of 14 ♀ were taken 24 March, 1946, and over 50 on various dates during March and April, 1949; 7 ♀ were taken in the light trap with the males. Most of the females were taken at platforms built in the trees, from 23 to 71 feet above ground level. A single specimen is also at hand from El Valle, Cocle Province, 16 June, 1946.

Stenotabanus frondicolus sp. nov.

Figs. 5, 5a, 5b

Length, 9.5–11 mm., wing, 10–11 mm. Frons dark golden yellow pollinose. Frontal callus black, nearly as wide as frons, gradually narrowed above into a slender ridge nearly reaching vertex. Vertical tubercle prominent, with 3 well marked ocelli, the vertex with unusually dense stout black setae. Eyes bare, in life bright brick red, with a single narrow green transverse band, fading on death to dull bronzy. Subcallus, fronto-clypeus and genae yellow pollinose, the last with sparse whitish beard. Antennae moderately slender, brownish, black haired. Proboscis short, much less than head height, but little longer than palpi, the labella fleshy.

Mesonotum blackish with four somewhat grey pollinose stripes, whose intensity varies with the light incidence. Hairs black on dark parts, brassy on the pale stripes. Scutellum pale pollinose, with dark hairs in the middle and brassy hairs around the margin. Pleura steel-grey pollinose, mostly pale haired, except a tuft of black hairs in the middle. Legs wholly black and black haired. Wings with subepaulet pointed and with fairly abundant macrotrichiae. Wings greyish hyaline with small but distinct clouds on fork of third vein and end of

discal cell. Abdomen above black in ground color, rather thickly overlaid with somewhat irridescent bluish pollinosity. This is very pronounced on the first tergite, less so on succeeding segments, where it is more or less confined to the posterior two-thirds of the tergites. The tergites are mainly black haired, except the first, which is wholly silvery haired at the sides. There is also a series of median silvery haired triangles on the second to sixth tergites and lateral patches of silvery hairs on the sides of the same tergites. Beneath the abdomen is black, mostly bluish pollinose and with all sternites with complete transverse bands of silver hairs. The insect in life bears a remarkable resemblance to a scarophagid fly.

This species belongs to a group including *tantulus* Hine, *muscoideus* Hine, *plenus* Hine and *modicus* Hine, differing from *tantulus* in the spotted wings and more slender antennae, from *muscoideus* in yellow antennae and slender palpi, and from *plenus* in more slender antennae and differently marked wings. From *modicus*, of which I have a specimen from French Guiana for comparison through the kindness of Dr. C. B. Philip, it differs structurally very little, the antennae being slightly broader, the frontal callus shorter. It lacks the white on the bases of the front tibiae found in *modicus*, while the latter lacks thoracic stripes and any abdominal ornamentation. It may well prove to be a race of *modicus*. *St. maruccii* Fchld. 1946 is also close, but may be separated from the present species on the thoracic ornamentation, the broader, more parallel-sided frons, and larger frontal callus.

Holotype female, Progreso, Chiriqui Prov., Panama, 20 July, 1950; 9 female *paratypes*, same locality, 16 June (1), 28 July (1), 3 August (3), 17 August (1), 31 August (1), 9 Nov. (1), 16 Nov. (1); 7 female *paratypes*, Sta. Fe, Veraguas Prov., Panama, 18–23 May (1), 29 May (1), 31 May (3), July (1), 10 Aug. (1).

With a few exceptions, all the specimens were taken at platforms built in the tree tops in heavy forest, from 36 to 83 feet above ground level.

Stenotabanus (Aegialomyia) ananasi sp. nov.

Figs. 6, 6a, 6b

Female.—Length 10.5–11.5 mm., wing 8.5–9.5 mm. Eyes bare, in life dull blackish with three dull greenish-bronze transverse bands. Frons greyish-brown pollinose. Frontal callus black or dark brown, quite protuberant and shiny, irregularly trilobulate above, wider than high and as wide as frons. No median callus or vertical tubercle, though in some specimens a small denuded area is discernible at the vertex. Subcallus, face and genae dull greyish brown pollinose, the genae with sparse pale hairs. Antennae yellowish brown, the first two segments with scattered black hairs, not produced above. Basal plate of third segment nearly round, the dorsal angle hardly evident. Annulate portion nearly as long as basal plate, the annuli stout. Palpi white, black and white haired, rather inflated. Proboscis short, hardly exceeding palpi, blackish, the labella membranous.

Mesonotum and scutellum light greyish brown, faintly striped, thinly clothed with short whitish hairs. Pleura and sternum pale greyish brown, sparsely white haired. Wings with subepaulet bare, costa and first vein with macrotrichiae above, but subcosta bare.

Wings hyaline including costal cell, but with a barely perceptible darkening around cross-vein and fork of third vein, which bears an appendix. Veins blackish, stigma pale yellowish. Legs wholly pale brown, mostly pale haired, though the tips of fore tibiae and all tarsi dark haired. Abdomen pale greyish brown, concolorous with thorax, the pollinosity paler along the hind margins of all tergites and with a paler middorsal pollinose stripe covering second to sixth tergite inclusive. The paler areas are covered with short silvery white hairs, the darker areas with blackish hairs. Venter similarly pale brownish, unmarked with sparse pale hairs.

Holotype female and four female *paratypes* taken attempting to bite the author along the beach between Old Fort San Lorenzo at the mouth of the Chagres river and the village of Pina, Colon Province, Panama, 23 May, 1948. Four female *paratypes*, Nuevo Chagres, Colon Province, Panama, 5 Feb., 1951, biting man on beach. The name is taken from the generic name of the Pineapple, *Ananas*, as Pina, the type locality, means pineapple in Spanish.

The species is quite close to *St. changuinolae* Fchld., and like it is related to *St. laevicallus* Szilady and *St. jamaicensis* Newst. From the first it may be separated by the more convergent frons, higher callus and more inflated palpi, and from the last two by unicolorous and differently shaped antennae, unicolorous legs and less obviously spotted wings. The eye pattern is rather different from *St. laevicallus*, more like that found in *St. psammophilus* O. S. from Florida.

Tabanus (Philipotabanus) keenani Fchld. 1946

A second specimen of this species (La Victoria, Cerro Jefe, Panama Province, Panama, 1 Sept. 1950, P. Galindo coll., taken at light in a Shannon trap) shows that the fourth tergite bears a broad silvery haired mid-dorsal triangle, and the sides of the second to fourth tergites also bear silvery hairs. The type is not now before me, but may have been rubbed, which would account for the absence of these easily lost hairs.

Tabanus (Philopotabanus) inauratus Fchld. 1946

Two additional females of this species (La Victoria, Cerro Jefe, 15 March, 1949, and Sta. Fe, Veraguas, 18 July, 1950) enable me to make some corrections and additions to the original description. The eyes are bright emerald green in life, not blackish green as stated. The former observation was made on a specimen dead several days. In addition to the patches of golden hairs on the mesonotum at the transverse suture, there are scattered golden hairs on the anterior part of the mesonotum. In addition to the white hairs on sides of first and second tergites, this patch is extended onto the anterior part of the third tergite. The venter is slate grey rather than black, black haired, but with scattered white hairs on middle of tergites I to IV.

Tabanus (Lophotabanus) fumomarginatus Hine

Figs. 7, 7a, 7b

Tabanus fumomarginatus Hine, 1920, Ohio J. Science, 20 (8): 315–316 (3 ♀; Rio Caiary, Vaupes, Amazonas, Brasil); 1925, Occ. Pap. Univ. Michigan, no. 162 p. 28 (in key only). Fairchild, 1942, Psyche, 49 (1–2): 16 (type seen).

Two ♀, La Victoria, Cerro Jefe, Panama Province, R. P., 6 and 16 May, 1950. These specimens agree well with Hine's description and with the notes I made on the type in 1940. The species is close to *pseudoculus* Fchld., but with a broader frons and more slender antennae. The face, frons and subcallus are golden yellow pollinose, the beard orange yellow and the palpi and legs orange haired, rather than black and white haired. The fore tibiae are not bicolored. The widening of the fore tarsi described by Hine is present, but other species of the group, as well as unrelated tabanids, also possess this character. The wings are quite fumose, especially the basal cells, costal area and along all veins. There is no appendix to the fork of the third vein and the first posterior cell (R_5) is hardly narrowed. The abdomen is dark orange brown, black haired dorsally except for small golden haired triangles on all tergites and copper haired lateral margins. Beneath the abdomen is wholly copper haired, except the extreme tip, which has upstanding black hairs.

Leucotabanus pauculus sp. nov.

Figs. 10, 10a, 10b

Female.—Length 8.5–9.5 mm., wing 7.5–9 mm. Frons about eight times as high as wide at base, broader at vertex, brownish grey pollinose. Callus club-shaped, black, narrower than frons and prolonged above in a slender line nearly to vertex. Vertical tubercle prominent, with prominent vestiges of ocelli. Subcallus yellowish grey, fronto-clypeus and genae silvery grey pollinose, the latter with sparse white beard. Eyes bare, probably unicolorous blackish in life. Antennae wholly black, as figured. Palpi rather slender, pale with greyish pollinosity and mostly white hairs, though there may be some black hairs intermixed, especially towards the tip. Proboscis about length of palpi, black, the labella large and without shiny sclerotized plates.

Mesonotum blackish, sparsely black haired on disk. Sides from the prothoracic lobes to and including the scutellum, pale greyish pollinose, white haired. Pleura and sternum pale greyish, sparsely white haired. A black-haired band extends forward from the wing bases to the anterior spiracle. Coxae, femora and tarsi all black, black haired. All tibiae with the basal two-thirds to three-fourths white and white haired. Wings hyaline or faintly fumose, the costal cell yellowish, stigma black. Subepaulet, costa, subcosta and first vein with macrotrichiae above; no appendix on third vein.

Abdomen above black and black haired. All tergites narrowly pale behind, but only the first, second and fourth with white hairs. On the first these are limited to the sides, on the second and fourth they form complete but narrow bands. First and second sternites largely greyish and white haired, the rest black with white haired hind marginal bands.

Holotype female, Curralinho, Para, Brasil, 1936, H. W. Kumm Coll.; 1 ♀ *paratype*, Tabatinga, Amazonas, Brasil; 1 ♀ *paratype*, Vaupes region, Colombia, April, 1942, Gast Galvis coll.

This little species keys out with *L. ambiguus* Stone and *canithorax* Fchld. in my key to the genus (1941). It differs from both in much

smaller size, unstriped mesonotum and in structures of the head. It superficially resembles *leucaspis*, but is smaller and with pale palpi and different frons and antennae.

Leucotabanus weyrauchi sp. nov.

Figs. 11, 11a, 11b

Female.—Length 11–13 mm., wing 10.5–11 mm. Frons about six times as high as basal width, pale-grey pollinose. Callus orange brown, drop-shaped, extended above in a narrow line nearly to vertex. (Through an oversight the figure shows the callus as black.) Vertical tubercle prominent, with hardly discernible traces of ocelli. Eyes bare, probably unicolorous blackish in life. Subcallus, fronto-clypeus and genae whitish pollinose, the last with a white beard. Antennae as figured, the first two segments reddish brown, black haired, the third segment wholly black. The prominently produced dorsal angle of the first segment and the wide and deeply excised third segment are characteristic. Palpi slender, yellowish white, white haired basally, black haired on about the apical half. Proboscis black, about as long as palpi, the labella large and without shiny sclerotized plates.

Mesonotum rather denuded in both specimens, light chestnut brown in ground color, apparently with four pale stripes, the median pair narrowly separated from each other. Sides of mesonotum and scutellum whitish pollinose, apparently with long white hairs, of which only vestiges remain. A few black hairs before the wing bases, hardly abundant enough to form a stripe. Pleura and sternum pale pollinose, white haired. All coxae, fore femora, tips of tibiae and tarsi blackish and black haired. Mid and hind femora, basal half of fore tibiae, and basal three-fourths or more of mid and hind tibiae orange yellow, white haired. Wings, including costal cell, hyaline; stigma slender, yellowish; subepaulet, costa, subcosta and first vein with macrotrichiae.

Abdomen light chestnut brown in ground color. First tergite dark haired dorsally, white haired at the sides. Second tergite with a broad mid-dorsal white triangle which barely fails to join the lateral white hind-marginal patches of the segment. Third, fifth and sixth tergites with smaller mid-dorsal white triangles and extreme lateral margins white haired. Fourth tergite with a white-haired transverse band three-fourths the width of the segment and wider at the middle and sides. Otherwise the tergites are black haired. The pollinosity appears to be pale brownish throughout, but it may be darker or sparser beneath the black haired areas. Beneath the abdomen is pale tan pollinose, wholly white haired. Terminal segment not laterally compressed as in *leuconotum* Fchld.

Holotype female, Zamora, Ecuador, Nov., 1941, D. B. Laddey coll.; 1 female *paratype*, Tingo Maria (Rio Huallaga), Peru, 700 M. alt., 7 Oct., 1946, Weyrauch coll. To be deposited in the M. C. Z.

This species seems most closely related to *leuconotum* Fchld., from which it may be distinguished by the much more prominent angle on the third antennal segment, which is black instead of orange brown, the more slender palpi, and somewhat different frons. In color they are very similar, but the present species seems to be paler and has even less black on the legs.

Leucotabanus leucogaster sp. nov.

Figs. 8, 8a, 8b

Female.—Length 11.5 mm., wing 11.5 mm. Frons about three and one-half times as high as basal width, yellowish grey pollinose. Callus black, as wide as frons, covering most of frons nearly to vertical tubercle. Vertical tubercle prominent with three well marked ocelli. Eyes bare, probably unicolorous blackish in life. Subcallus, frontoclypeus and genae white pollinose the last two with long white hairs. Antennae blackish brown, the third segment rather slender. Palpi whitish, white haired at base, black haired at apex, the hairs rather long and outstanding. Proboscis black, the large labella fleshy.

Mesonotum pale brownish with darker streaks in ground color, completely covered with white pollinosity and apparently with white hairs, though most of these are now lost. Pleura, sternum, scutellum and coxae white and white haired. Femora dusky, black haired at apex and on upper surface, white haired at base and on under surface, the relative amount of black hairing greater on the fore femora. Tibiae white and white haired on basal half to three-fourths, black and black haired apically, as are all tarsi. Wings with subepaulet rather sparsely setose, the macrotrichiae mostly white. Costa, subcosta and first vein with macrotrichiae above. Wings hyaline including the costal cell, but with very faint clouding about the cross-veins and fork of the third vein, which bears a minute vestige of an appendix. Stigma broad, yellowish.

Abdomen blackish in ground color, covered with whitish pollinosity. All tergites are black haired basally and bear broad, complete, transverse hind-marginal bands, wider in the middle and at the sides, of long silvery white hairs. Venter dark grey, dark haired except for narrow white haired margins to all sternites.

Holotype female, Itatiaya, Est. Biologica, 22 Jan., 1927, 1100 M. Alt. Sao Paulo, Brasil.

This species is close to *albibasis* Brethes, being practically identical in size and color. The frons is rather broader, however, and the callus, although of the same type, is much more extensive, while the third antennal segment is considerably more slender. It is possible that this is but a mountain form of *albibasis*, but more material would be needed to decide the point.

Tabanus (Taeniotabanus) picicallosus sp. nov.

Figs. 9, 9a

Female.—Length 10 mm., wing 8.5 mm. Eyes (relaxed) bluish green with two narrow, median, transverse bands and the margins dark purple, bare. Frons yellowish grey pollinose, the pollinosity more brownish in the area of the median callus, black haired.

Frontal callus black, rather flattened and wrinkled, (though this character not well shown in the figure) more or less quadrangular; median callus spindle-shaped, connected to the basal by a slender line in one specimen, more broadly in the other. No vertical tubercle. Subcallus black, shiny, greatly inflated, separated from the basal callus by a pollinose area about half the height of the latter. Face

and cheeks grey pollinose, white haired. First antennal segment yellow, black haired, triangular and quite strongly inflated. Second not as wide as first, with a blunt tooth above. Third wholly orange yellow, the basal plate quite broad, the dorsal angle obtuse. Annuli together about half length of basal plate. Palpi not as long as proboscis, moderately inflated, light grey pollinose and black haired. Proboscis less than head height, brownish, the labella large and membranous.

Mesonotum blackish, thinly greyish pollinose, paler anteriorly and with sparse golden and blackish hairs forming indistinct stripes. There are also scattered irridescent scale-like hairs. Scutellum concolorous. Pleura and sternum grey pollinose, sparsely white haired. Legs wholly yellowish; all coxae white haired; fore femora wholly black haired, mid and hind femora black haired above, pale haired below. Fore tibiae silvery white haired on basal half, black haired on apical half, mid and hind tibiae black haired above, pale haired below; all tarsi brownish, black haired. Wings dilute smoky, more intense beyond stigma along fore border. No appendix on fork of third vein. Abdomen black, the first and second segments very dark reddish brown, all black haired except for a narrow continuous mid-dorsal white stripe from first to sixth tergites, slightly widened on the hind margins of the tergites, and broken, narrow, white dorsolateral stripes on the first to third tergites. Sides of tergites narrowly white. Venter slate grey, mostly white haired.

Holotype female, Tingo Maria, Peru, 670 M. alt., April, 1947, Weyrauch coll.; 1 ♀ *paratype*, same locality, January, 1947.

This species differs from all others of the *callosus* group known to me in the broader frons and combination of pale legs, black abdomen and fumose wings. It will run in my key (1942, p. 155) to *fumatipennis* Kröb., from which it can be separated by the wholly pale legs and much broader frons.

Tabanus pruinosus Bigot

1892, Mem. Soc. Zool. France, 5: 683 (♂, Mexico). Philip, 1947, Amer. Mid. Nat., 37 (2): 312 (synonymy, type seen); 1950, Ann. Ent. Soc. Amer., 43 (1): 116, fig. 2c (antenna and palp).

Tabanus vivax Townsend 1892, Trans. Kansas Acad. Sci., 13: 135. Not *T. vivax* O. S., 1876.

Tabanus limpidipennis Hine 1907, Ohio Nat., 8: 223 (♂, ♀; Guatemala).

? Tabanus schmidti Kröber, 1931, Konowia, 10 (4): 292 (♀; nr. San Jose, Costa Rica); 1934, Rev. Ent., 4 (3): 314.

A single female (Bambito, Chiriqui Volcano, Chiriqui Prov., Panama, Jan., 1948) has the following characters. Eyes entirely bare, in life purple with two parallel transverse green bands. Frons moderately broad, about three and one-half times as high as wide, with a rounded brown callus. Vertical tubercle represented by a shiny area showing sunken vestiges of three ocelli. Subcallus pollinose, without hairs. Antennae black, the first segment rather inflated. Palpi inflated basally, slender tipped, pale brownish, clothed with mixed white and black hairs. Proboscis black, a little longer than palps, the labella large and fleshy. Wings with subepaulet, costa, subcosta and first vein setose, no appendix on fork of third vein, entirely hyaline with a yellowish

stigma. Legs pale brown, white haired, except the apices of fore and hind tibiae and all tarsi, which are darker and black haired. Pleura, sternum and venter of abdomen brownish, thickly pale grey pollinose, the pleura and sternum densely whitish haired. Mesonotum brownish grey, obscurely striped, with long black and short sparse coppery red hairs mixed, the latter following the light stripes. Scutellum blackish. Abdomen blackish brown, with faint narrow middorsal triangles, and the hind margins of tergites 2–5 pale grey pollinose. There is also a series of rounded grey pollinose dorsolateral spots on tergites II-VI, larger on the second. The mid-dorsal triangles bear a few yellow hairs, the dorsolateral spots are white haired, otherwise the abdomen is black haired above.

This species is rather unlike any other in Panama, being closest structurally to *Hybomitra 4-punctatus* Fab., from which it differs mainly in the entirely bare eyes. The relationship lies with a group of Nearctic species recently discussed by Philip (1950). The vertical tubercle, although hardly raised, shows better definition of the vestiges of ocelli than do many species of *Hybomitra*, so that it could be placed here without question were it not for the entirely bare eyes. I had determined the specimen as *T. schmidti* Kröber from the description, but Dr. Philip after examining it writes me that it is *pruinosus* Bigot. The two names are probably synonymous. I have also seen another specimen, also determined by Dr. Philip, from the West Coast of Nicaragua, erroneously reported by me as *T. dunni* Fchld. (1942, p. 472). *Pruinosus* thus ranges from Mexico south to western Panama.

Tabanus lucidulus Walker

1848, List Dipt. Ins. Brit. Mus., 1: 188. Bequaert, 1940, Rev. Ent., 11 (1–2): 347–349, fig. 28 (synonymy).

While in Jamaica in the spring of 1949, I had the opportunity, through the kindness of Mr. C. B. Lewis, the Curator, to examine the Tabanidae in the collections of the Institute of Jamaica in Kingston. There was a pair of what I take to be *T. lucidulus* Walk. as well as a considerable series of *T. townsendi* Johns. The female *lucidulus* (Morces Gap, St. Andrews, 22 Aug., 1942, L. Perkins Coll.) measured 13 mm. in length, hence larger than any measurements for this species given by Bequaert (1940, l.c.). It agreed, however, with his description and figures, except for having an orange brown beard. A considerable series of the same species taken attacking a horse at Cornpuss Gap, St. Thomas, 27 May, 1949, by Dr. Trapido and myself are all small, 11 mm. or less, and have sparse whitish beards. The male specimen in the Institute's collection (Cinchona, St. Andrew, 29 Aug., 1942, J. C. Jury coll.) is even larger, 14 mm., in this agreeing with *obumbratus* Bequaert. It agrees in coloration, however, with the female from Morce's Gap, including the orange brown beard. The subepaulet bears macrotrichiae, the eyes are entirely bare, the area of enlarged facets a little over one-half the eye area and fairly well demarcated from the small facets. There is no vertical tubercle. The wings are paler than in the female, hardly infuscate, the spotting weak, and there is no appendix on the upper fork of the third vein.

The collection of fresh material of *lucidulus* shows the eyes to be bronzy in life with a single quite broad median black band. The abdomen, even in the freshest specimens, is quite thinly clothed, subshiny, dull yellowish brown, paler on the anterior segments, clothed with sparse dark hairs, and with broad whitish haired median triangles on the first to sixth tergites. These triangles do not appear to reach the anterior border of the segment except on the second tergite. The wings are rather variable in my series, some being quite yellow with clearer fenestrae in some of the cells, others paler and without fenestrae. The spotting of the cross veins is weak in all, barely perceptible in a few specimens.

Stenotabanus (Aegialomyia) jamaicensis (Newstead)

Atylotus jamaicensis Newstead, 1909, Ann. Trop. Med. Parasit., 3: 465.

Three specimens of what appear to be this species, hitherto known only from the types, were taken on Palisadoes beach, Kingston Harbor, Jamaica, 23 May, 1949. The day was windy and the flies scarce and hard to net. They rested on the grey sand of the beach at high tide mark, flying up like Cicindelidae on one's approach. They made no attempt to bite. Mr. Lewis informed me that they had been quite abundant there earlier in the year. Subsequently Mr. Lewis sent me a specimen taken on North East Morant Cay, 20 June, 1949. This is a small island lying about 45 miles South East of the eastern tip of Jamaica.

All these specimens agree among themselves. Compared to the descriptions of *laevicallus* and *jamaicensis* given by Bequaert (1940) they agree best with the former. My smallest specimen is 11 mm., the largest 14 mm. The eye in life is pale glaucous green, almost pearly, crossed in the middle by two narrow bands of reddish purple which coalesce near the outer margin of the eye. The upper and lower margins are also largely reddish purple, somewhat intermixed with greenish. The specimens are wholly steel grey in color, thickly pale grey pollinose and wholly pale haired. They appear quite brownish when greasy, a condition developing quite frequently in species of this group, especially when stored in the tropics. My notes were made on the fresh material.

The only marked distinctions between the two species seem to be the eye color and the size. Newstead may have drawn his description from a relaxed or not freshly caught specimen. Port Royal is on the tip of Palisadoes beach, so my material is practically topotypical. More extensive material of this group of Antillean beach-inhabiting species may well show that all belong to a single species with more or less well marked insular races.

REFERENCES

Barretto, M. P. 1946. Estudos sobre Tabanidas Brasileiros. II. Sobre o genero *Catachlorops* Lutz, com descricoes de sete especies novas. An. Fac. Med. Univ. S. Paulo, 22: 151–183, 29 figs.

1948. Estudos sobre Tabanidas Brasileiros. V. Sobre o genero *Amphichlorops* Lutz, com as descricoes de quatro especies novas. Rev. Ent., 19 (3): 401–417, 8 figs.

1948. Estudos sobre Tabanidas Brasileiros. VIII. Sobre os generos *Dichelacera* Macq. e *Rhamphis* End., com a descricao de un novo genero. An. Fac. Med. Univ. S. Paulo, 24, 63–80.

Bequaert, J. 1940. The Tabanidae of the Antilles. Rev. Ent., 11 (1–2): 253–369, 33 figs.

Enderlein, G. 1925. Studien an Blutsaugenden Insekten 1. Grundlagen eines neuen Systems der Tabaniden. Mitt. Zool. Mus. Berlin, 11 (2): 255–409, 5 figs.

Fairchild, G. B. 1940. Notes on Tabanidae from Panama. II. The genus *Dichelacera* and related genera. Ann. Ent. Soc. Amer., 33 (4): 683–700, 2 plates.

1941. Notes on Tabanidae from Panama. IV. The genus *Leucotabanus*, and VI. The genus *Fidena*. Ann. Ent. Soc. Amer., 34 (3): 629–638 and 639–646, 2 plates.

1942. Notes on Tabanidae from Panama. VII. The subgenus *Neotabanus*. Ann. Ent. Soc. Amer., 35 (2): 153–182, 2 plates.

1942. Notes on Tabanidae from Panama. IX. The genera *Stenotabanus* Lutz, *Lepiselaga* Macq. and related genera. Ann. Ent. Soc. Amer., 35 (3): 289–309, 1 plate.

1946. Additional notes on the Tabanidae of Panama. Ann. Ent. Soc. Amer., 39 (4): 564–575, 1 plate.

Kröber, O. 1929. Neue Tabaniden und Zusatze zu bereits beschriebenen. Zool. Anz., 90 (3–4): 69–86, 20 figs.

1929. Die Pelecorynchinae und Melpiinae Sudamerikas. Mitt. Zool. Mus. Hamburg, 44: 149–196, 33 figs.

Philip, C. B. 1950. New North American Tabanidae. Part II. Tabanidae. Ann. Ent. Soc. Amer., 43 (1): 115–122, 2 figs.

RECENT ADVANCES IN THE STUDY OF THE ORIENTATION OF THE HONEY BEE, by K. von Frisch. Bulletin of Animal Behavior, No. 9, pp. 1–33, March, 1951.

An important contribution to the controversial subject of communication among insects was made by the publication by Professor von Frisch, in 1946, of "Die Tanze der Bienen" (Oesterr. Zool. Zeitschs, 1: 1–48), in which he sets forth the hypothesis that the honey bee worker can indicate, by her dance on the honeycomb after her return to the hive, the direction and distance of food from the hive. This paper was translated into English and thus appeared as "The dances of the bees" in the Bulletin of Animal Behavior (London), no. 5, December, 1947. Professor von Frisch's ideas have received wide attention both in the press and through a motion picture film, made under his direction, which has had wide distribution among scientific audiences in the United States. The Bulletin of Animal Behavior is to be commended for making available in English, not only the original article on the dance of the bee, but also translations of selections from three other articles, which appeared under the above heading. These include "Solved and unsolved problems of the bee language" ("Geloste and ungeloste Ratsel der Bienensprache"), 1948, Naturwiss. 1: 12–23 and 2: 38–43, translated in full; "The polarization of light from the sky as an orientating factor in the dances of the honey bee," ("Die Polarisation des Himmelschlichtes als orientierender Faktor bei den Tanzen der Bienen"), 1949, Experimentia, 5: 142–148; and "The Sun as a Compass in the life of the honey bees," ("Die Sonne als Kompass in Leben der Bienen"), 1950, Experientia, 6: 210–21.—M. T. J.

A SIMPLIFIED BIOLOGICAL ASSAY METHOD USING THE COCKROACH, PERIPLANETA AMERICANA (LINN.), FOR PROTEIN UTILIZATION[1]

JANICE F. SIEBURTH,[2] MARY GAIL BONSALL,[2]
AND
BARBARA A. McLAREN[2]

Studies on cockroaches have been limited largely to their habits, physiology and biology, and methods of control. However, the use of the cockroach, *Blatella germanica*, as an assay animal for nutritional studies has been proposed recently. Noland, Lilly, and Baumann (1949) studied the nutritional requirements of the cockroach, using test tubes and about five nymphs to a cage. Reproducible results were obtained when growth was measured by weighing each group to within 0.5 mg. at ages of 10, 20, and 30 days. Daily records were kept of age and sex of maturing individuals. House and Patton (1949) reared *B. germanica* under aseptic conditions, using cages constructed from Kolle flasks. The nymphs were weighed individually and growth evaluated by weight increment. House (1949) developed a chemically-defined diet by this method. Gier (1947) reared *Periplaneta americana* in glass culture dishes at 30° C., feeding the stock colony *Purina Dog Chow Pellets*. He found that this roach has 10 instars and that there are 16 eggs in the normal oothecum. Gould and Deay (1938) studied the biology of the American cockroach, rearing them in battery jars and feeding raw potato. Gould and Deay (1940), and Bottimer (1945, found dog biscuits and pablum satisfactory for raising cockroaches.

The purpose of this paper is to describe a simple and practical method for rearing the cockroach, *Periplaneta americana*, under controlled conditions as an assay animal for nutritional studies. Data of experiments on rate of growth of the cockroaches fed different proteins are included. The application of this method to nutritional studies is valuable, since only a small amount of material for diets, technical labor, and time is necessary.

PROCEDURES

Stock Colony.—The stock colony consisted of adult American cockroaches (*P. americana* (L.)) obtained from a supply house[3] in New York. They were kept in groups of approximately 50 in wide mouth gallon jars covered with 100 mesh wire screen. Filter paper was cut to fit the bottom, and water was supplied in three-inch crystallizing dishes inverted over watch glasses. Cones of filter paper were furnished for shelter, and jars were kept in an incubator at 30° C.

---

[1]Scientific Paper No. 1053, Washington Agricultural Experiment Stations, Institute of Agricultural Sciences, The State College of Washington, Pullman. Cost of publication is paid by the above institution.

[2]Department of Home Economics, The State College of Washington, Pullman.

[3]Ward's Natural Science Establishment, Inc.

All jars were cleaned, and fresh food and water were supplied weekly. Ootheca were gathered at this time and transferred to vials loosely plugged with cotton.

Experimental Colony.—Each oothecum hatched 14 to 16 nymphs. Those from one egg capsule were placed in a half-pint jar set up the same as the jars for the stock colony, except that water was supplied by small vials laid on their sides with plastic lids plugged with a wick. Prepared diets were packed in small pieces of glass tubing sealed at one end.

Weighing.—Weighing and cleaning were done weekly. To facilitate handling, the cockroaches were anaesthetized with carbon dioxide, and

TABLE I

COMPOSITION OF DIETS

Component	1 %	2 %	3 %	4 %	5 %	6 %	7 %	8 %	9 %	10 %
Whole Milk Powder	25									
Whole Egg Powder	25									
Whole Wheat Flour	50									
Casein		10	25	50						
Honey Protein					10	25	50			
Gluten								10	25	50
Sucrose		75	60	35	75	60	35	75	60	35
Crisco		8	8	8						
Wesson Oil		2	2		10	10	10	10	10	10
Hubbell Salts[4]		5	5	5	5	5	5	5	5	5
Cod Liver Oil				2						

[4]Hubbell, *et al.* (1937).

the entire group was weighed with a torsion-type double hook balance to within 0.2 mg. The average weight of an individual cockroach was then determined.

Experimental Diets.—*Purina Laboratory Chow* was the diet used for the control groups. Experimental diets are listed in Table I. All food was supplied *ad libitum*. A crude diet of whole milk powder, whole egg powder, and whole wheat flour was fed to the second control group. To determine the optimum protein level, three diets of 10, 25, and 50% vitamin-free casein were fed.

Each experimental diet was supplemented with the following vitamins per 100 grams of diet: 50 μg. thiamine, 50 μg. riboflavin, 250 μg. calcium pantothenate, 580 μg. nicotinic acid, 20 μg. choline, 50 μg.

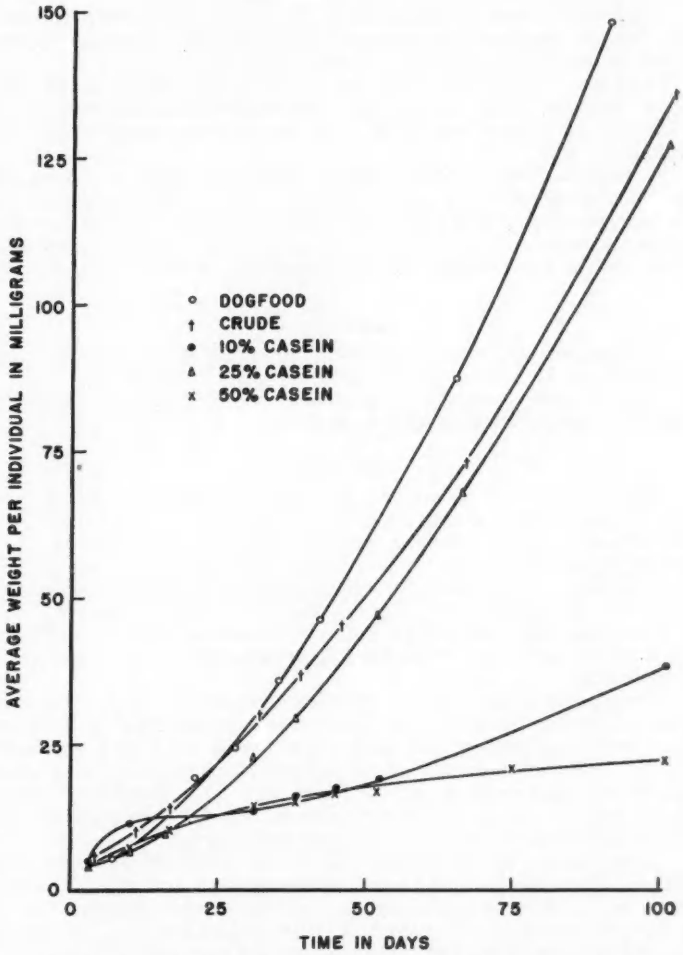


FIG. 1. Growth of nymphs on dogfood, a crude diet, and a purified diet containing three levels of casein.

pyridoxine, 130 μg. inositol, 250 μg. p-aminobenzoic acid, 100 μg. mixed tocopherols, 0.05 mg. biotin, 50 mg. ascorbic acid, 330 I. U. vitamin A (Oleum A liquid), and 33 I. U. vitamin D (viosterol).

Similar diets were prepared, using the protein from wheat (gluten) and honey to compare the biological value for the cockroach. These proteins were extracted in the following manner:

1. Gluten: Gluten was obtained by making a dough which was allowed to stand for 15 minutes and then washed with cold water until practically no starch remained. The protein was then dried and ground in a mill.

2. Honey: 200 g. of honey were diluted with water to 1 liter and then saturated with ammonium sulfate crystals. The solution was left for approximately 48 hours, the protein skimmed off the surface and dialyzed against water. The dialysis product was reprecipitated with 70% alcohol, centrifuged, and the separated protein was dried and ground.

RESULTS

A comparison of the growth of nymphs on dogfood, a crude diet, and purified diets containing three levels of casein is shown in figure 1. In figure 2, similar curves are illustrated for diets containing casein, honey, and gluten as the source of protein.

DISCUSSION

The cockroach, *P. americana*, was easily reared and required little care or equipment. Purina Dog Chow supplemented with fresh liver was found to give optimum growth rate and reproduction. The ootheca produced by the stock colony were used for the nutritional studies. The 14 to 16 nymphs from each egg capsule provided one group for an experimental diet, and several of these groups were used in measuring each diet. Five grams of ration were usually sufficient for an experiment, and this aided in storage as well as in reducing cost of materials.

From figure 1 it can be seen that cockroaches on a diet of dog food show an excellent growth rate. Those on the crude diet of whole wheat flour, whole egg powder, and whole milk powder fell slightly below the dog food diet. The growth on the purified food containing 25% casein closely approximated that on the crude diet. Ten and 50% levels of casein showed a sharply depressed growth rate. It was apparent that 25% casein best fulfilled the protein requirement for this cockroach.

A comparison of the growth rate on the 25% level of casein with that on three levels of the proteins from honey and wheat is shown in figure 2. It is obvious that the growth of the cockroach on the gluten and honey protein was much below that on casein. The nymphs on diets containing the lower levels of the honey protein (10% and 25%) showed no appreciable growth over the one-hundred-day period. Diets with the highest level of honey and lowest level of gluten enabled the insects to grow at a rate approximating one-third that on 25% casein. The two highest levels of gluten improved the diets to such an extent that the cockroaches on those diets grew about half as well as the 25% casein. It is apparent that the cockroach is very sensitive

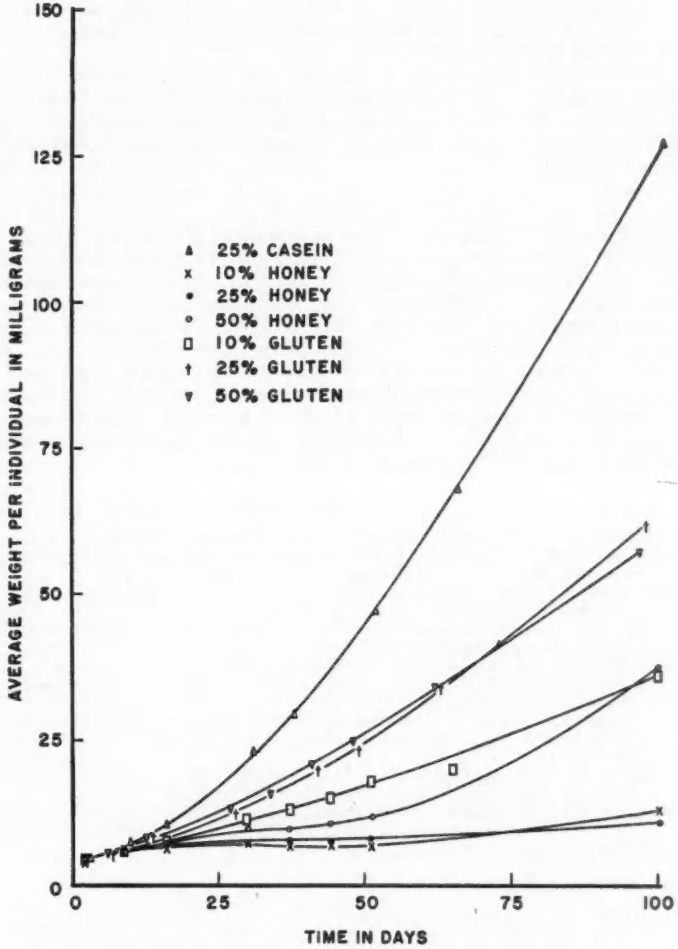


FIG. 2. Growth of nymphs on diets of 25% casein and three levels of gluten and honey protein.

to protein quality and is, therefore, able to differentiate between different proteins. It is interesting to note that in these experiments there appeared to be an optimum level for casein protein. Such a relationship for gluten and honey did not seem to exist at the level fed. Thus it appears that the deficiency of essential amino acids is quite critical for the cockroach.

These results may serve to illustrate the value of insects like the cockroach as experimental animals, *e.g.*, the protein in honey amounts to only about 3%, and with higher animals the cost and time required for the preparation of a sufficient quantity for a nutritional study would be prohibitive.

SUMMARY

A simple and practical method is described for rearing the cockroach, *Periplaneta americana*. The growth rate on dogfood is compared with that on a crude diet as well as on purified diets with different levels of casein. The growth on three levels each of gluten and honey protein showed a very low biological value for the honey; slightly higher for the gluten; but both considerably lower than casein.

The data from the series of experiments reported in this paper in which cockroaches were used to evaluate proteins from different sources show remarkably well the ability of the cockroach to measure protein quality. Similar studies are being carried on in this laboratory, using this cockroach for other assay procedures.

LITERATURE CITED

Bottimer, L. J. 1945. Roach rearing and testing. Soap San. Chem., 21: 151–157.

Gier, H. T. 1947. Growth rate in the cockroach, *Periplaneta americana* (Linn.). Ann. Ent. Soc. Amer., 40: 303–317.

Gould, George E., and **Howard O. Deay.** 1938. The biology of the American cockroach. Ann. Ent. Soc. Amer., 31: 489–498.

1940. The biology of six species of cockroaches which inhabit buildings. Purdue U. Agric. Exper. Sta. Bull. no. 451.

House, Howard L., and **Robert L. Patton.** 1949. Nutritional Studies with *Blatella germanica* (L.) reared under aseptic conditions. I. Equipment and technique. Can. Ent., 81: 3.

House, Howard L. 1949. Nutritional studies with *Blatella germanica* (L.) reared under aseptic conditions. II. A chemically defined diet. Can. Ent., 81: 105–112.

Hubbell, R. B., L. B. Mendel, and **A. J. Wakeman.** 1937. A new salt mixture for use in experimental diets. Jour. Nutr., 14: 273–285.

Noland, Jerre L., J. H. Lilly, and **C. A. Baumann.** 1949. A laboratory method for rearing cockroaches and its application to dietary studies on the German roach. Ann. Ent. Soc. Amer., 42: 63–70.

ENZYMES IN INSECTS. ACID PHOSPHATASE[1]

MORRIS ROCKSTEIN AND LEONARD LEVINE[2]
Laboratories of Zoophysiology, State College of Washington, Pullman[3]

Examination of a recent important review by Metcalf (1948) reveals that, aside from earlier reports on the studies of the effects of toxic materials upon *digestive* enzymes, very little work concerned with the biochemical basis for insecticidal action has been attempted, except for considerable recent research involving the enzyme important in the transmission of nerve impulses, cholinesterase. Literature concerning this enzyme has been reviewed in reports by Rockstein (1950), Metcalf and March (1950) and Chamberlain and Hoskins (1951). It is apparent that, for a deeper understanding of the actual mechanism of action of many of our newer insecticides, fundamental quantitative studies are needed on other enzyme systems important in the intermediary metabolism of normal insects. In this connection, Sacktor (1950) has adapted for quantitative study in insects the important respiratory enzyme, cytochrome oxidase, which should provide a useful enzyme system for further study. Various other scattered reports concerning enzymes in insects on one phase of intermediary carbohydrate metabolism have been cited in a review by Rockstein (1950a).

It is the object of this brief report to present data on the activity of the enzyme acid phosphatase in five different species of insects, all of which are commonly reared and employed in a wide variety of laboratory studies. Phosphatases are important in vertebrates in protein formation, carbohydrate metabolism, bone repair and calcification and in the formation of nuclear protein material. The occurrence and importance of phosphatase have been discussed in two important reviews by Moog (1946) and by Roche (1950). The chemistry of phosphatase in insects has been studied quantitatively by Fitzgerald (1949) in grasshopper eggs and in the adult worker honey bee by Rockstein and Herron (1951), each employing different biochemical procedures.

Table I gives the median enzyme activity from five incubation replicates[4] from a single homogenate of a specified number of individuals. In the case of the two species of flies and the American roach, the insects were immobilized by storage at 5° C. in a cold room, for 10

[1]This investigation was supported in part by funds provided for biological and medical research by the State of Washington Initiative Measure No. 171. Publication costs are also paid from the above funds.

[2]Graduate research assistant.

[3]The authors acknowledge their appreciation to Mr. Herman Menke, Apiculturalist of the State College of Washington, for his kind assistance and fine cooperation in making available colonies for this study. To Dr. A. W. Lindquist, of the U.S.D.A. at Corvallis, Oregon, are due thanks for supplying pupae of non-resistant house flies.

[4]In the case of *P. sericata* six replicates from a common homogenate were used.

minutes immediately prior to homogenizing; both drone and worker bees were decapitated first; mealworms were rinsed, dried, weighed and then homogenized directly. The homogenizing and enzyme procedure are discussed in detail by Rockstein and Herron in a forthcoming paper (1951). For acid phosphatase study, 3 ml. of brei (homogenate), 3 ml. of 2% sodium β-glycerophosphate buffered by 0.848% sodium barbital, 1 ml of 0.3 *M* acetic acid, and 1 ml. of 0.08 *M* $MgCl_2$ were incubated in ground-stoppered tubes for 1½ hours at 35° C., at a pH of 5.4. Following inactivation by heat, protein precipitation with 1 ml. 30% trichloroacetic acid, and filtration, enzyme activity was spectrophotometrically determined, by means of the adaptation by Rockstein and Herron (1951a) of Sumner's (1944) ferrous sulfate phosphomolybdic method for estimating phosphate as phosphorus. This

TABLE I

ACID PHOSPHATASE ACTIVITY IN SEVERAL SPECIES OF INSECTS

Species	Age	Average Body Weight in Mg.	Measured Activity in μg. P/0.2Ml. /1.5 Hrs.	Activity in Mg.P/Gm. Body Weight/Hr.
Apis mellifera L.				
Worker*	<48 hr. adult (20)*	113.5	7.90	1.480
Drone	<46 hr. adult (5)	142.0	29.20	20.500
Musca domestica L.	<23 hr. adult (25)	9.9	2.56	5.180
Tenebrio molitor L.	2.7 cm. larva (20)	213.9	3.40	0.398
Periplaneta americana (L.)	"Adult" (5)	888.6	2.02	0.227
Phaenicia sericata (Meig.)	<44 hr. adult (25)	17.5	0.0015	0.0017

*Figures in parentheses represent number of homogenized individuals in 50 ml. of final homogenate (brei) mixture.

**Data by Rockstein and Herron (1951).

involves colorimetric determination employing 0.2 ml. samples of the experimental, control, or standard phosphate solutions, 9 ml. of acid molybdate, and 0.8 ml. of Sumner's ferrous sulfate solution. Determinations were made in the model B Beckman spectrophotometer at a wave length of 720 mμ.

In examining Table I, one should note that the data in the last vertical column on the right are expressed in ***milligrams*** of phosphorus released, per gram of fresh body weight, per hour. The raw data, as directly determined colorimetrically, are given in the vertical column immediately to the left of the above, and are expressed as ***micrograms*** of phosphorus in 0.2 ml. samples of protein-free incubating mixture, released in 1½ hours. From these latter values it is apparent that *Phaenicia sericata*, with two replicates giving zero activity, would prove a poor animal species for future studies of this enzyme, because of its low activity as studied by this method. In the case of the adult

house fly and mealworm larvae, as well as the American roach, increasing the number of individuals per lot to be homogenized would be desirable to raise the value of the raw data. This would be readily practicable in the case of the roach with obviously high activity per whole animal. It is further apparent that in this connection, the drone as well as the worker honey bee show reproducible raw data of very high to moderate value.

In terms of enzyme activity per gram of fresh body weight, however, the drone honey bee, with a relatively high average body weight, and the house fly, with the smallest average body weight of all five species, show the greatest enzyme activity; *P. sericata* shows the least and the American roach a very low activity. The implications of these comparative values cannot be suggested without a great deal of further study of the enzyme in each species. However, the tremendously greater activity of the enzyme in the drone, compared to any other insects studied in this laboratory, may be related to several findings by workers, reported in a current review by Mann and Lutwak-Mann (1951), that there is a relatively high acid phosphatase activity in the semen of mature male mammals. In this connection, the exact data of sexual maturity of drone honey bees is apparently still unknown, although drones normally do not *function* as males until considerably later than a week and usually at about two weeks after emergence of the adult. Since this high activity was observed in drones of average age of about 23 hours, the possible relation of this enzyme to sexual maturity in male honey bees would be a matter of interesting future study. A histochemical study of phosphatase in the honey bee (drone and worker) is planned for the coming year in this laboratory.

From the point of view of ease of rearing and handling all species except *P. sericata* would lend themselves to further research involving this enzyme. However, determination of enzyme activity of *each sex*, which was attempted only in the case of the honey bee in this study, would be desirable. It is the authors' own opinion that the honey bee, with its rather universal availability, easy natural separation of sexes, and relatively high enzyme activity, is superior to the other four species reported upon herein, as a laboratory animal in studies on this enzyme. The fact that carbohydrate metabolism is especially important in the adult honey bee suggests further that this enzyme may be an important starting point for fundamental enzymological or for toxicological studies concerned with this metabolism in this insect.

SUMMARY

Acid phosphatase activity is reported for five species of insects, including drone and worker honey bee, the common house fly, the yellow mealworm, American roach and *Phaenicia sericata* (Meig.). Activity values for *P. sericata* were found to be too low to permit practical future study by the method employed; the highest activity expressed in terms of fresh body weight was found to obtain for the drone honey bee. Activity values obtained for the roach, house fly, mealworm and both sexes of the honey bee indicate that these four species could be readily employed in future studies concerned with acid phosphatase.

LITERATURE CITED

Chamberlain, W. F., and **W. M. Hoskins.** 1951. The inhibition of cholinesterase in the American roach by organic insecticides and related phosphorus-containing compounds. Jour. Econ. Ent., 44: 177–191.

Fitzgerald, L. R. 1949. The alkaline phosphatase of the developing grasshopper egg. Jour. Exp. Zool., 110: 461–487.

Mann, T., and **C. Lutwak-Mann.** 1951. Secretory function of male accessory organs of reproduction in mammals. Physiol. Revs., 31:: 27–55.

Metcalf, R. L. 1948. The mode of action of organic insecticides. Natl. Research Council Chem.-Biol. Coordination Center Rev. No. 1, Wash., D. C.

Metcalf, R. L., and **R. B. March.** 1950. Properties of acetylcholine esterases from the bee, the fly and the mouse and their relation to insecticide action. Jour. Econ. Ent., 43: 670–677.

Moog, F. 1946. The physiological significance of the phosphomonoesterases. Biol. Revs. Cambridge Phil Soc., 21: 41–59.

Roche, J. 1950. Phosphatases. *In* The Enzymes, edited by **J. B. Sumner** and **K. Myrbäck.,** Vol. I, Pt. 1, Academic Press, New York.

Rockstein, M. 1950. The relation of cholinesterase activity to change in cell number with age in the brain of the adult worker honey bee. Jour. Cell. Comp. Physiol., 35: 11–24.

1950a. Glycogen metabolism in insects: A review. Bull. Brooklyn Ent. Soc., 45: 74–81.

Rockstein M., and P. W. Herron. 1951. Phosphatase in the adult worker honey bee. (To be published.)

1951a. Colorimetric determination of inorganic phosphate in microgram quantities. Anal. Chem. (In press.)

Sacktor, B. 1950. A comparison of the cytochrome oxidase activity of two strains of house flies. Jour. Econ. Ent., 43: 832–838.

Sumner, J. B. 1944. A method for the colorimetric determination of phosphorus. Science, 100: 413–414.

ERRATUM

Distenia bougainvillea Gress. (Ann. Ent. Soc. Amer., **44**: 3, 1951) is a synonym of *Distenia bougainvillea* Schwarzer (Deut. Ent. Zeit. 1923: 255). The correction was mailed to the editor from China after the manuscript was submitted, but it apparently never reached him.

A GLOSSARY OF TERMS AND PHRASES USED IN THE STUDY OF SOCIAL INSECTS

ALBRO T. GAUL
Department of Biology, Long Island University,
Brooklyn 1, New York

This glossary developed as a result of the author's personal need for definitions of terms and phrases used in the study of the social insects. It has been suggested that such a glossary might be of service to others in the same field and in related fields. It is hoped that this paper will serve such a need.

The emphasis of this glossary is on terms relating to social conduct and relationships and other biotic phenomena as they are encountered among the social insects. Taxonomic and morphological terms have been omitted, except in those instances where it is believed that because of their peculiar identity with the social species, such terms should be included.

The author is under no misapprehension that this glossary is complete or exhaustive. Although no terms have been purposefully omitted, it is quite likely that many terms may not have been encountered by the author, and hence are missing.

For purposes of brevity, most terms appear in only one form. No effort has been made to list the noun, adjective, verb or adverbal forms of the same root word. It is assumed that the reader can supply such prefixes or postfixes as may be necessary.

In most cases the authorship of terms has been neglected. In many instances, authorship is difficult to trace, and frequently of slight significance. Wherever new, rarely encountered, or dually defined terms appear, some attempt has been made to show such authorship.

A

Acid gland. One of a pair of filiform glands opening by a duct into the poison sac of aculeate Hymenoptera.

Acron. First segment of an ant (Jardine).

Adelphogamy. The mating of sister with brother.

Alates. Sexually mature individuals with wings.

Allometrosis. The presence of different species of social insects, or of different races of gynes in one colony at one time (Forel).

Alpha female. An intermediate in structure between teratogyne and normal female. (Wheeler). The normal queen when it coexists with the aberrant Beta female (Imms).

Amazons. Obligatory slave making ants of the genus *Polyergus*.

Amical selection. The process by which true guests of ants and termites have developed from symphiles (Wassman).

Ammochaetae. Long, forward directed hairs on the lower surface of the head, used in cleaning and dusting the strigils.

Ampherotocous. Parthenogenesis in which unfertile eggs develop into either male or female. Same as **Deuterotoky.**

Androgynous. Uniting the characters of both sexes.

Aner. The true male form of a species.

Annual colony. A colony in social Hymenoptera which lasts for only one season and dies out at its end.

Anthophila. Species with dilated and pubescent hind tarsi, the Bees.
Anthophilous. Flower loving. Seeking pollen, nectar or both.
Antidzierzonists. Those who doubt the validity of Dzierzon's Rule. See **Dzierzon's Rule.**
Aphidicolous habit. The habit of attending aphids in order to imbibe the secreted honey-dew.
Apivorous. Bee eating.
Apterergate. A wingless worker in a species of normally winged workers (Vespids).
Apterogyne. A wingless female in a species of normally winged females.
Apterous forms. (Termites) Ergatoid kings and queens. (In general) Any wingless form.
Arenicolous association. Association of a species with a sandy habitat.
Arrhenotocous. Parthenogenesis in which infertile eggs become males.
Autotrophallaxis. The drinking of trophallactic secretion by the larva producing it.
Auxiliaries. The slaves in mixed colonies of slave making ants.

B

Beta female. See **Teratogyne.**
Biocenosis. The association of individuals of different species.
Biota. The total flora and fauna comprising insects and the plants with which they are associated.
Bivouac. The periodic resting place of doryline ants (Schneirla).
Blastophthory. The entire change in the heredity of, "all that can no longer be crossed or modified by individual acquisition or education, or even deteriorated by germ poisoning" (Forel).
Brachypterous forms. Neoteinic termites. Specifically kings and queens.
Bromatia. The growths of fungi which are cultured as foodstuffs by ants and raised upon the substrate.
Brood. All the young of a social species. Specifically: All the young at a like age level in any colony of ants (Schneirla).

C

Caespiticolous association. Species preferring to nest in grassy pastures, lawns or fields.
Callow. a teneral individual.
Calobiosis. A form of symbiosis in which one species, or the queen of one species, lives in the nest of, and at the expense of, another species, either temporarily or permanently (Smith).
Calyptodomous. Having a nest enclosed in an envelope.
Campestral. Inhabiting fields.
Cannibalism. A condition in which individuals devour members of the same species as themselves. General: A condition in which adults devour their brood. Among Vespinae: The condition encountered toward the end of the colony life, or under abnormal circumstances, in which the adults kill or eat all or part of the larvae and pupae.
Cap. The silk covering of a brood cell by the prepupa; it is frequently continuous with a silk cell lining.
Carton. The paper manufactured by Hymenoptera for nest construction.
Carton nest. The type of nest built by *Nasutitermes*, constructed of lignin, fecal matter and wood remnants.
Caste. That difference in forms which distinguishes fertile individuals from workers.
Cell. A small, frequently hexagonal structure, often made of paper or wax, which is incorporated in the nest structure. It is utilized in brood production and food storage. The aggregate of the cells in any one stratum is a comb.
Cenosis (also **coenosis**). See **Biocenosis.**
Centris. The sting in Hymenoptera.
Cerago. Bee bread.
Cerumen. The mixture of wax, earth and resins found in the structure of the nests of the stingless bees (*Trigona*).
Cespiticolous. See **Caespiticolous association.**
Chemotactic sense. Supposed appreciation of chemical differences by means of touch. Presumed as a factor in behavior of some ants.

Chordotonal organs. Organs in the tibiae of some ants, thought to be organs of hearing.
Chrymosymphily. Friendly relations between ants and lepidopterous larvae, based upon the attractive scent emitted by the larvae.
Cleptobiosis. A thief-host relationship, wherein the thief steals food from foraging workers of another species.
Clustering. The habit of gathering in groups prior to mating (Fernald) or prior to hibernation, or due to low temperature (Rau) observed among *Polistes* wasps.
Coccidicolous. Having the habit of feeding on honey-dew secreted by coccids.
Coenobiosis. A definite consociation of animals and plants of different species.
Colacobiosis. Permanent social parasitism.
Comb. A stratum of single or double cells used for the storage of food or for the rearing of brood in the nests of social bees and wasps.
Commensal. A species which feeds on surplus supplies of another, but without harming the host.
Communal. Living or dwelling in colonies.
Compound nest. A nest containing more than one species, where the brood is kept separately.
Consocies. In ecology, groups of mores, usually dominated by one or more in agreement as to main features of habitat preference, time of reproduction, reaction to physical factors, etc. (Shelford).
Corbicula. Pollen basket of certain bees of the podilegous type.
Cryptogyne. Name applied to females who are superficially indistinguishable from the workers.

D

Dart. A sting.
Daubing. A process in which an intruder into a colony is soaked with liquids from the mouth. A defensive action of bumblebees when rejecting an intruder of superior fighting ability.
De-alation. The loss of wings by adult insects. It occurs among termites and female ants.
De-alate. To lose the wings. An insect which has lost its wings.
Defaunated. The loss of symbiotic intestinal protozoa (by termites).
Degenerate slave makers. Slave making ants who permit the host female to live and continue egg production, thus forming mixed colonies.
Dendrophile. A species or individual living in woody tissue or trees.
Dendrophilous. Condition of living in woody tissue.
Depauperate colony. An impoverished or declining colony of social insects.
Deportation. The carrying of adults to a new nest, or the carrying of young inexperienced workers to the old nest from the field. This may be an extension of the habit of carrying the brood.
Deserticolous association. Preference for living in deserts or dry plains.
Desmergate. An intermediate form between soldier and worker (ants).
Detritivorous. Feeding on fur or feather detritus.
Deuterotoky. A type of parthenogenesis in which either males, females or both may be produced.
Diacammatogyne. Workers of the genus *Diacamma* which take the place of normal females.
Dichthadiigyne. A form found among the Dorylinae only, an oversexed form of gynaecoid with no eyes, ocelli, or wings and with a large gaster and ovaries.
Dinergate. A member of the soldier caste in ants.
Dinergatogyne. A mosaic form combining the characteristics of soldier and ergatogyne. A hyperfeminized soldier.
Dinergatogynomorph. An individual in which female characteristics alternate with worker characteristics and soldier characteristics.
Dinophthisergate. A soldier-worker mosaic which never changes from pupa to imago from parasitic, disease, or other causes.
Diploergate. A mosaic individual embracing characteristics of both major and media workers.
Diploptera. The group of vespoid wasps whose fore wings are longitudinally folded.
Diplopteryga. Synonym of Diploptera.
Dorylaner. An aberrant macraner found among the Dorylinae, with unusually large modified mandibles, cylindrical gaster and singular genitalia.

Drone. The male adult of *Apis mellifera* L.
Dufour's gland. The gland which produces the alkaline element in the sting of the social Hymenoptera.
Dulosis. A relationship wherein one species makes slaves of the workers of a colony of another species.
Dzierson's Rule. The supposed rule for sex determination among social Hymenoptera wherein all fertilized eggs become female and all unfertilized eggs become male.

E

Ecphorized smell. See **Topochemical sense.**
Embryogenesis. The genesis of the species through the egg (Forel).
Emmet. An ant.
Endophytic. Living within plant or tree tissue.
Epigaeic. Species preferring to live on the surface of the earth. Living above ground.
Epimegetic. A major worker.
Eremobiotic. Living under conditions where there are no ants (Farquharson).
Eremophilous. Deserticolous, living in arid or desert regions.
Eremosymbiont. A species living in an ant nest, neither taking nor receiving nor contributing to the society but living in it for protection. These species are usually ignored by the hosts.
Ergatandromorph. A mosaic form combining the characteristics of worker and male.
Ergatandrous. Having workerlike males.
Ergataner. A dimorphic, apterous, ergatoid male.
Ergate. (Ants) The wingless, sexless worker form. (Bees and Wasps) The smaller, sterile, winged females. Workers. (Termites) The wingless workers of any sex. See also **Neuters, Operariae, Workers.**
Ergatogynandromorph. A feminized worker, a gynandromorph with ergate qualities.
Ergatogyne. A female with mosaic worker like characteristics.
Ergatoid. A normally functioning female with a worker like thorax.
Ergatoid complemental. A termite worker functioning as a reproductive.
Ergatomorphism. Having the appearance and form analogous to the worker.
Ergatotelic. A method of colony reproduction in which the foundress female flies with her sister workers to found a new colony. The workers construct the new nest while the female merely exhibits the secondary sex attributes of her solitary ancestors. Swarming.
Ergepitropic. Supplying food and caring for the brood (Goeldi).
Ericeticolous association. Preference for living in sandy, gravelly, or sparsely covered soil exposed to the sun.
Eumegetic. A media worker or ergate.
Eurythermal ubiquists. Ants which flourish under differing temperature conditions.
Eutrophapsis. The habit in which the female brings prey or food to the young in a previously prepared nest.
Extranidal. Outside the nest.
Exudatorium. A gland or process secreting an exudate. Exudatoria are found on the bodies of termitophiles and Myrmecophiles, and on the larvae of some social species. The secretions of the exudatoria are agreeable to the host.

F

Facultative slavery. The making of slaves by ants who can survive without slaves (Wasmann).
Fission. The splitting of a social colony for any purpose.
Formicary. An ant nest or colony.
Formicarium. An artificial ant nest.
Fourmiliere double. Colonies comprising more than one species, in which the brood is kept separate by species.
Fourmiliere mixtes. Colonies comprising more than one species, in which the brood is mixed.
Fusion. The uniting of two or more colonies of a species into one colony.

G

Gallicolous. Living in galls, whether the producer of the gall or as a guest or inquiline of the gall.
Gastrilegous. Having pollen baskets under the abdomen.
Gonepitrophy. Carrying out sexual functions (Goeldi).
Gongylidia. Hyphal modifications of the fungi which are cultivated by the Attine ants.
Granivorous. Grain or seed eating.
Guest. An insect living in nests of other species. It may be among any of the categories in the host-guest relationships.
Gymnodomous. Having a nest with exposed or uncovered combs, as in *Polistes* or *Mischocyttarus* (Bequaert).
Gynaecaner. A gynaecomorphic male appearing in some workerless and parasitic species of ants. It resembles the female in having the same number of antennal joints.
Gynaecoid. A worker differing from the normal in the physiological ability to produce eggs.
Gynaecotelic. Having a foundress female whose instincts involve all the sexual attributes of the solitary ancestral species. That method of colony reproduction in which the young queen founds her nest without the aid of workers (see **Ergatotelic**).
Gynandrarchy. A social organization founded by both male and female, usually with the fertile forms living together for some time.
Gynandromorph. A mosaic form combining the characteristics of male and female, possibly but not necessarily an hermaphrodite.
Gynarchy. A social organization in which the female is the foundress and dominant figure.
Gyne. A true, normal female.
Gynecoid. See **Gynaecoid.**
Gynergate. A mosaic form combining worker and female characteristics.

H

Hamabiosis. Compulsory, advantageous symbiosis (Janet). Symbiosis in which there is no apparent motive or advantage (Bueno).
Haplometrosis. Foundation of a new colony by a single fertile queen or female.
Haplometrotic. Monogynous (Bequaert).
Hermaphrodite. Having characteristics of both sexes.
Hermaphroditism, primary. An individual with organs of both sexes developed.
Hermaphroditism, secondary. In which the female fertilizes her eggs subsequent to initial insemination by the male (Forel).
Heteroecism. The changing of hosts (Wasmann).
Heteroecious. Living with different hosts at different periods of the life history (Wasmann).
Heterogyna. The ants, based upon the different types of females found.
Hibernaculum. The place of hibernation or overwintering.
Honey. The thick, partly dehydrated, liquid prepared by bees from nectar.
Honey pot. The individual wax cell for the storage of honey, found in the nests of bumblebees.
Hyphaenosymphily. A synoeketic relationship between lepidopterous larvae and ants, based upon the spinning of silk by the larvae.
Hypogaeic. The habit of living underground the major part of life, but always coming to the surface for the nuptial flight.
Hypomegetic. A minor worker.

I

Incubation. The hatching period of an egg (Bueno). The instinctive clinging of the queen or worker bees to the brood cells during cool periods (Plath).
Infrasocial. Below any social level. Solitary.
Inquiline. A type of social parasite, in which the invading female kills the female host, and rears her own young with the help of the host workers. Usually the inquiline species has no worker forms of its own.
Integral symbiosis. Obligatory symbiosis for both symbionts (Forel).

Intermediate. A symmetrical individual blended of two castes. A symmetrical mosaic.
Ioterium. The poison gland or sack of the Hymenoptera (Kirby & Spence).
Isoparthenogenesis. The normal parthenogenesis (Henneguy). Arrhenotoky.

K

Kinaesthetic sense. Perception of distance.
King. A male termite who is the cofounder of the colony.
Kinopsis. The appreciation of moving objects which would otherwise remain unnoticed if stationary.

L

Lammert's cycles. The nearly daily cycles of temperature rise and fall in bees' nests during winter. They are ascribed to increased activity and consequent oxidation of sugar.
Lapidicolous association. Preference for living under deeply imbedded stones.
Leadership. Heading or leading the movement in a column of ants (Schneirla).
Leadership relations. See **Peck order.**
Lestobiosis. The permanent thief-host relationship, wherein a small species of ant nests near a larger, host species enters the galleries of the host to purloin food (Forel).
Loricate synoekete. A synoekete with broad shoulders and tapering, hard, body, whose external form prevents the easy grasping of their bodies by their hosts.

M

Macraner. A large form of male which frequently appears in populous colonies.
Macrergate. A large worker form often appearing in populous colonies.
Macrocephalic female. A large headed female, presumably an alpha female. See **Alpha female.**
Macrogyne. A large female form.
Macrophthalmic. Having large eyes, or having eyes larger than normal. (Wheeler).
Macropseudogyne. A female with vestigial or short wings, broader or more convex mesonotum, caused by infestation of *Lomechusa* in the colony.
Macropterous. Having large wings.
Macropterous female. A long winged female, presumably an alpha female. See **Alpha female.**
Macropterous forms. True kings and queens among the termites (Imms).
Major. A large sized worker, the largest of a polymorphic series, an epimegetic.
Malaxation. The process or act of chewing. The grinding of cellulose fibers in the mouth prior to paper making by the paper wasps.
Mandibulates. The large soldier termites.
Maximae. The larger worker ants, majors, epimegetics. See **Major.**
Meconium. The pellet of accumulated wastes discharged by the larva just prior to pupation among the ants, bees and wasps.
Mediae. The medium sized worker in a polymorphic series, an eumegetic.
Megetic. Size variation of a particular caste based upon quantitative larval feeding.
Meliphagous. Honey eating.
Melittophile. Any guest, parasite or predator in the society of bees.
Milleferous. Honey making or producing.
Merithaner. An anomalous form of male parasitized by Mermethid worms in the gaster.
Mermithergate. An anomalous form of worker parasitized by *Mermis* worms.
Mermithized. Condition of being parasitized by nematodes of the genus *Mermis*.
Mermithodinergate. An anomalous soldier form, parasitized by *Mermis* worms. Synonyms: **Mermithostratiodes** and **Mermithophore.**
Mermithogyne. A female parasitized by *Mermis* worms.
Mermithophore. See **Mermithodinergate.**
Mermithostratiotes. A mermithized soldier (Vandel). See **Mermithodinergate.**
Mesopsuedogyne. Similar to the macropseudogyne but somewhat smaller and having a convex or humped mesonotum.
Metochy. Relation of ants to tolerated guests in their nests. There is no apparent exchange between the guest or its hosts.
Micraner. A small type of male.

Micrergate. A dwarf worker, usually the first worker brood of a young colony.
Microcephalic female. A small headed female, presumably a beta female. See **Beta female.**
Microgyne. A dwarf female form.
Micropseudogyne. Similar to a macropseudogyne, but differing in its smaller size.
Micropterogyne. A female form with small wings. It may be a normal form for some species.
Micropterous female. A short winged female, presumably a beta female. See **Beta female.**
Mimesis. Mimicry.
Mimetic synoekete. A synoekete which mimics its host in color, form or pilosity.
Minimae. Smaller worker ants, hypomegetics, minors. See **Minor.**
Minor. A small sized worker, the smallest of a polymorphic series, hypomegetic or minima.
Mixed nest. A colony composed of more than one species, in which the brood of each species is not separated. See **Fourmiliere double.**
Mixtobiosis. Any condition in which nests contain more than one species. Condition of having compound nests.
Monodomous. Condition of having, or living in, only one nest.
Monogynous. A gnyarchic colony having only one foundress female in the colony.
Monometrosis. The state of having only one female in a colony.
Monomorphic. Having only one form of worker, although these may vary in size.
Mosaic. A form of individual in which the characteristics of more than one sex or polymorphic form may be evident, either symmetrically or asymmetrically, *i.e.*, gynandromorphs, ergatoids, etc.
Mycetometochy. A form of social symbiosis between fungi and the inhabitants of compound nests.
Mycetophagus. Fungus eating.
Myrmecochorous seeds. Seeds having attractive properties to ants.
Myrmecocleptics. A synoekete which steals food from its ant hosts while two such hosts are exchanging food or sharing food (Janet).
Myrmecology. The study of ants.
Myrmecophagic. Myrmecophiles which feed on ants (Janet).
Myrmecophile. The parasites or commensals of ants which live within the nests of the hosts.
Myrmecophily. The relationship between ants and another organism in which the ants act as the hosts.
Myrmecophyte. A plant having phytophilous relations with ants.
Myrmeophile. See **Myrmecophile.**
Myrmecoxene. A true guest or symphile of ants, where the relationship is beneficial to both species.

N

Nasute. A worker termite with vestigial mandibles and whose head is drawn forward into a tube for the ejection of defensive liquids.
Natural requeening. The continuance of a colony upon the death or loss of the foundress female, by the entrance of another female of the same species as in *Bombus* (Plath).
Nemoricolous association. Preference for dwelling in sunny woodlands, marginal woodlands or clearings.
Neoteinic. A newly developed king or queen termite functioning as a substitute reproductive.
Nest aura. The individual odor of a particular nest.
Nest wall. The nest envelope. The layer or layers of carton surrounding the colonies of wasps.
Neuter. An inappropriate term for sterile castes, a loose term for worker or ergate.
Neutral synoekete. An insect which pays little attention to its hosts, but lives on and eats the refuse of a colony.
Nomadic phase. That part of the colony cycle of the doryline ants in which a daily shifting of location of the colony is undertaken.
Nuptial flight. The flight of sexual forms for mating purposes.
Nutricial castration. The loss of fertility through selective feeding during the larval period by the brood nurses. The basis of the theory of the trophogenic determination of caste.

O

Obligatory slavery. The making of slaves by ants who are never found without slaves (Wasmann).
Oecotrophobiosis. Trophallaxis (Roubaud). **See Trophallaxis.**
Oligophagous. Restricted in range of food plants.
Oligotrophic. Species which only feed upon or frequent a single genus or species of plant.
Operariae. Workers, ergates, megetics. See **Ergate.**
Orphan nest. A nest containing live brood but no adults (Rau).
Ovarian castration. The formation of workers from the females of a species through overwork and reduction of the ovaries.

P

Panmixia. Genetic swamping (Wheeler).
Parabiosis. Tutelage, phylacobiosis (Forel). The special relationship between *Crematogaster parabiotica* F. and *Dolichoderus debilis parabiotica* F. (Forel). The condition in which two species have intermingled nest chambers or galleries, but do not behave like a compound colony (Smith).
Parasitoidism. A condition in which the larval stage is an ecto- or endoparasite upon the brood of another species, and in which the infested host dies.
Paroecismic. Plesiobiotic.
Parthenogenesis. The development of an egg into a normal individual without fertilization by a spermatozoon.
Partial symbiosis. A condition in which one species, apparently dependent upon another, can actually survive alone; or a situation in which both species can survive independently, but prefer to associate.
Pavillons. The sheds of cells built by ants as a shelter for their plant lice.
Peck order. A form of social behavior. The prerogative of individual A to push aside individual B who can, in turn, push aside individual C, etc. The development of a social hierarchy (Schjelderup-Ebbe).
Pellet. The ball of food, earth or paper pulp carried in the mouth by vespines.
Permanent social parasite. A relationship wherein the parasitic species produces no worker forms of its own. It depends on successful raids of other societies for its workers. This relationship differs from inquilinism in that more than one colony of the host species may be the victim of the parasite. It is characterized by the development of soldiers in the parasitic species.
Perennial colony. Any colony which lasts from season to season.
Phoresy. Being carried from one place to another by another species (Janet).
Photodermatic sense. The perception of light through the skin without eyes (Forel).
Phragmocyttarous. Having nest combs supported by the nest wall or envelope.
Phragmosis. Habit of closing the nest entrance with the anterior portion of the head (Wheeler).
Phthisaner. A pupated male form which never develops into an imagine because of parasitism.
Phthisergate. A pupated worker form which never develops into an imagine because of parasitism.
Phthisogyne. A pupated female form which never develops into an imagine because of parasitism.
Phthisodinergate. A pupated soldier form which never develops into an imagine because of parasitism.
Phylacobiosis. Tutelage or parabiosis. A relationship between two species in which they may nest together, even to the extent of having interconnecting galleries for mutual protection, but rearing the brood separately. The situation in which *Camponotus mitarius* nests with termites (Wasmann).
Physergate. Large workers, capable of egg production but used for honey storage.
Physiological division of labor. The division of labor in a colony according to differences in physiological function.
Physogastric. A female with a greatly enlarged abdomen for mass egg production, as in termite queens.
Phytophily. The trophic relations between insects and plants.
Pleometrosis. Having more than one fertile queen. See **Polygyny.**

Plerergate. The replete worker of the honey ant, *Myrmecocystus*.
Plesiobiosis. A neighborly protective relationship between colonies of differing species, in which the weaker colony is protected by its nearness to the stronger colony.
Pleural lobes. The fleshy processes of the lateral abdominal segments of the larvae of the vespine wasps which are used to hold the larvae in the brood cell.
Pleurergate. A worker ant capable of distending its gaster with liquid food until it becomes nearly spherical.
Podilegous. Having pollen baskets on the legs.
Podometric sense. The sense that measures the extent of walking (Pieron).
Poecilandry. Having more than one form of male.
Poecilocyttarous. The type of nest of the social wasps in which the comb is built around a support and covered by a nest wall.
Poecilogony. See **Polymorphism.**
Poecilogyny. Having more than one form of female.
Polyandry. The condition in which one female has more than one male mate.
Polycalic. A large colony consisting of mother nest and a number of subsidiary nests (Forel).
Polydomous. Having a number of fungus gardens in different cells or galleries (Weber). One society living in more than one nest at the same time.
Polygyny. A gynarchic social structure in which many females function at the founding of the colony, or in which a single foundress female and one or more of her daughters may preside over the colony. Pleometrosis.
Polymorphism. A condition in which more than sexual differences adapt individuals of a species to the performance of several specialized tasks. The condition of having specialized workers of more than one morphological class; not to be confused with simple size differences between workers.
Polyspermy. The entering of more than one sperm into an egg. Suggested as a possible cause for mosaics and anomalies (Huettner).
Polytropic. A species which visits a number of genera or species of plants.
Pratinicolous association. Having the preference of inhabiting low, grassy meadows or bogs.
Primary allometrosis. The alliance of females of different species to found a single colony (Wasmann).
Proctodeal food. Food passed from anus to mouth by adult termites.
Propolis. Bee resin, particularly that of *Apis mellifera* L.
Protelian social parasitism. See **Temporary social parasitism.**
Proto-cooperation. Activities which may be regarded as helpfully incidental to fundamental physiological facilitation.
Protodichthadiigyne. A highly fertile intermediate between ergatoid and dichthadiigyne (Wheeler).
Psammophilous. Sand loving.
Pseudogyne. An apterous worker-like ant with the size and gaster of the worker, and thoracic development of the queen.
Pseudonest. A gathered mass of nest building material frequently found around the entrance to Bombus nests. Sometimes used to shelter workers.
Pseudopodia. A long segmented appendage holding bee larvae to food packets.
Pseudosymphile. A predator or parasite which nourishes itself at the expense of the trophallactic secretions of the host larvae.
Psychogenesis. The development of mind. The origin and development of social (and other) instincts and habits.
Pterergate. A worker with vestigial wings, form a species with normally apterous workers.
Pterine pigments. Those pigments deposited on cuticular areas of relatively low metabolism, notably in the vespine wasps.
Pterodinergate. An individual of the soldier caste with vestigial wings.
Pupillary parasitism. Slavery. See **Dulosis.**

Q

Queen. The inept term for the tertile foundress female of a colony.
Queen nest. The nest built by the founding queen of a monometrotic species prior to its enlargement by the first worker brood.

R

Radicicolus. Living exclusively on roots.
Replete. The worker of the honey ants (*Myrmecocystus*) which is specially adapted with an enlarged gaster for the storage of honey. A plerergate.
Reproductive. Adult, non-sterile insects.
Royal chamber. The space reserved for the accommodating of king and queen termites, or the space reserved for the queen of a gynarchic society.
Royal jelly. The liquid secreted by the pharyngeal glands of worker bees, which is used for food for the young larvae. It may contain gonadotropic hormones. Its presence or absence in larval diet may be in part, or in whole, responsible for trophogenic caste determination.
Royal pair. The king and queen termites. In general, the sexually active male and female social insects.

S

Saxicolous association. The preference for living in stony or rocky terrain.
Scopa. The brush-like structure in bees, used for collecting pollen.
Secondary somatic hermaphrodite. An insect with one pair of gonads for one sex, but with one or more secondary sex characteristics of the other sex.
Secondary pleometrosis. The presence of a number of queens of one species in a nest. This occurs by three processes: the alliance of colonies, the adoption of alien queens of the same species, and the breeding of females from the same colony.
Seed crushers. Dinergates with large heads and strong jaws, adapted for crushing seeds.
Sensomotility. The supposed sense of ants which permits the appreciation of turning without external data (Forel).
Silvicolous association. The association of a species with the typical moist shady forests of the temperate regions.
Social. Individuals which live in organized communities of the same species.
Social facilitation. The result of any increment or decrement in an individual's behavior resulting from the presence of another organism.
Social hierarchy. See **Peck Order.**
Social parasite. Any one of the species which feeds upon the stored products or upon the individuals of a community.
Social population. The number of individuals in a society in terms of density.
Lowest Density = Total Population/Area of Census.
Economic Density = Total Population/Territory occupied.
Greatest Density = Population of community at night.
Social symbiosis. The relationship in which one species feeds on food stored by a host species, thus injuring the latter (Bueno).
Sociocentric. Having a life centered about the community.
Soldier. A dinergate or major worker ant. A sexually undeveloped termite with falcate mandibles of considerable musculature and with large heads.
Solitary. Living alone, infra-social.
Spado. The ergate or neuter in the nest of an ant or bee (Bueno).
Specophile. Predators, parasites or guests in the nests of wasps.
Statory phase. Permanent nesting place in colony cycle of doryline ants.
Stelocyttarous. A nest in which the horizontal comb is arranged stratum upon stratum, with each stratum suspended from the next by a certical suspensor or partition; the combs are out of contact with the nest wall.
Stenothermal. Having the ability to live within a narrow range of cold temperatures.
Sterile. Incapable of reproduction.
Sting. The modified ovipositor of the Aculeate Hymenoptera which is used as a defensive and trophic mechanism. It is closely associated with the poison gland, whose secretion is injected into the prey by the dart.
Stomodeal food. The partly digested food which is transferred from mouth to mouth by adults.
Strepsiptera. An order of insects which in some species are parasitic upon some social insects. Stylops.
Strigilators. Synoeketes which feed upon the body secretions or saliva of the hosts.

Stylopized. Infested with Strepsiptera.
Stylops. The insects of the Order Strepsiptera.
Subsocial. Living in colonies but having individual nests. Living together in a general area, but without social organization or specialization of labor.
Substitute king. A complemental male termite.
Substitute queen. A complemental reproductive female termite.
Substrate. The material, frequently fecal matter or leaf parts, upon which ants raise fungi.
Succursal nest. The permanent resting or hiding place built by workers, but not a true nest as no brood is reared in it.
Suspensor. The column or partition of carton or wax attaching strata of comb in the nests of bees and wasps.
Swarming. A method of colony reproduction in which a fertile female and her worker escort from the parent colony migrate to establish a new social organization. Ergatotelic.
Symbiogenesis. The development of symbiosis.
Symbiont. An organism living in a condition of mutual exchange with another organism, of another species.
Symbiosis. The relationship between individuals of two species, living together in close association, usually to mutual advantage.
Symphile. A true or welcomed guest in a social group.
Symphiloid synoekete. A synoekete which is treated as a symphile, usually by possessing gustatory or olfactory secretions which appeal to the host.
Symphily. The relationship between symphile and host.
Synclerobiosis. Mixed nests of uncertain origin or meaning (Wasmann). The association of two species which are usually independent. The reasons for the association are indefinite (Smith).
Syndiacony. The relationship between ants and plants wherein both obtain some benefit from the other (Forel).
Synechthrans. The persecuted intruders into the nest of a host species.
Synechthry. The relationship between a social host species and the intruders who succeed in establishing themselves despite efforts of the host to be rid of them.
Synoecy. The relationship between social insects and their indifferently tolerated guests.
Synoekete. The indifferently tolerated guest of a social group. See **Mimetic, Synoekete, Loricate Synoekete, Symphiloid Synoekete, Strigilators** and **Myrmecocleptics.**
Syntrophy. The feeding of symphiles or synoeketes by accident while caring for the brood. The feeding relationship between ants and mites, in which the mites feed on ants salivary secretions while the ants are licking their eggs.

T

Tachygenesis. The acceleration of otogenic development (Wheeler).
Temporary social parasite. A relationship in which the parasitic queen invades a host colony, and by killing the parent queen, can use the services of the host workers until she can produce her own workers. This differs from Inquilinism in the fact that the parasitic queen eventually does produce worker forms, while it differs from Permanent social parasitism in having forms other than soldiers.
Teratogyne. A dimorphic female ant without wings. A Beta female.
Termitarium. The nesting place of termites, whether natural or artificial.
Termitophile. A synoekete or symphile of a termite colony.
Territoriality. The instinct for homing or deference of a given area. It has the following advantages: 1—Well spaced aggregations; 2—Promotion of monogamy; 3—Limitation of breeding; 4—Provides for a reserve of unmated sexual forms; 5—Insures adequate food supply; 6—Reduces the number of parasites; 7—Increases the knowledge of a locality, and 8—Increases the vigor of defense.
Thamnophilous association. Preference for dense thickets or vegetative areas.
Thelytocous. The form of parthenogenesis in which unfertilized eggs become female.
Topochemical smell. The supposed sense of smell permitting the appreciation of location through chemical emanations.
Trogolodytic. Living underground exclusively. See **Hypogaeic.**

Trophallaxis. The mutual exchange of food between larvae and adults.
Trophic symbiosis. The relationship between ants and other animals which are sought and cared for by the ants, for the benefit of the secretions or food that the ants can obtain. Example, ants and aphids. See **Myrmecophlly.**
Trophidium. The first larval stage of the genus *Pseudomyrma*.
Trophobiont. An organism living either within or without the nest of a social species, who is cared for and protected by that species. In return, the organism yields attractive secretions for the social insects.
Trophobiosis. The trophic relationship of ants to other insects outside the colony (Wasmann). See **Trophic symbiosis.**
Trophogeny. The determination of caste differences by nutritional mechanisms.
Trophoporic field. The habitat or area supplying the colony with food. See **Territoriality.**
Trophothylax. The pocket-like invagination in the first ventral abdominal segment of the larvae of the Pseudomyrminae. It is used to store food for the workers.
Turner's circling. The circling of the homecoming insect as it approaches the nest entrance.
Tutelage. Parabiosis. See **Phylacobiosis.**
Tutelary parasitism. See **Temporary social parasitism.**
Tyloid. A swelling or tubercle, often in pairs or groups, on the ventral surface of the terminal antennal segments of the male social wasps.

V

Venom. The secretion of the accessory, or poison, gland of the female aculeate Hymenoptera. The fluid injected as a sting. In the bee the venom contains apitoxin and histamine, in the ants it contains formic acid. See **Sting.**
Vesparium. The natural or artificial nest of a colony of vespine wasps.

W

Wax. The secretion of the wax glands of the bees which is used in nest structure.
Workers. Ergates, operatiae, megetics, etc. See **Ergate.**

X

Xenobiosis. An hospitable relationship between two societies, in which individuals from one society are welcomed as guests in the colony of the other society.
Xerophilous association. The preference for living in arid places.
Xerothermic fauna. That fauna which is found in warm, dry conditions (Forel).
Xylophagous. Feeding on woody tissues.

THE FUNKHOUSER COLLECTION OF MEMBRACIDAE

The William D. Funkhouser collection of the homopterous family Membracidae has been presented by Mrs. Funkhouser to the University of Kentucky, Lexington, the institution where the last thirty years of his life were spent. This accumulation of nearly forty years is the result of much personal exploration extending throughout the United States and girdling the world, supplemented by exchanges from many homopterists and from museums everywhere.

Three cabinets and 120 Schmitt boxes contain this outstanding collection, one of the best in the world, consisting of unknown thousands of specimens, representing 1267 species and most of the recognized genera. There are about 260 types covering the greater part of the species named by Funkhouser himself, mostly holotypes, with a few allotypes. Many paratypes have been retained, few of which solely represent their species in the cabinets.

It is desired that the collection be made as useful to the homopterist fraternity as possible, therefore this announcement. Principal types will be available to qualified *visiting* students of the group by prearrangement at any time. In case of species represented by a sufficient number of paratypes, reasonable numbers may be sent on loan to such qualified students with the usual appropriate guarantees. There is no one at the University of Kentucky who will undertake determinations or comparisons with types.

An additional advantage to visiting scholars will be the unique Funkhouser membracid library housed with the insects. It is probably as nearly complete as any in existence, containing the pertinent papers of such classical authors in the field as the following: Fabricius, Stål, Berg, Amyot and Serville, Fairmaire, Goding, Buckton, Walker, Kirby, Kirkaldy, Funkhouser, and others, some of which were laboriously copied long-hand or by typewriter in foreign libraries, before the day of photostatic reproduction or microfilm.

There is on hand here a large number of undistributed reprints of papers on Membracidae by Dr. Funkhouser, even many copies of his early Cayuga Lake report. These are to be made freely available on request by any interested entomologist who will write the undersigned.

It will be of interest to the profession that the Funkhouser fascicle of GENERA INSECTORUM, on the family Membracidae, has appeared, a volume of 383 pages with 14 plates. Unfortunately the more than 250 colored drawings prepared for the book have been issued in black and white. The manuscript of the work was submitted to the Wytsman publishing house in Belgium more than ten years ago and lay in storage throughout the war and until after the author's death, its fate unknown to him. It has had no subsequent revision.

Gifts of specimens and authors' separata are solicited so that the collection need not lose the "dynamic" character which it has always possessed.

The following is a list of type specimens in the collection. The asterisks (*) indicate allotypes, a few without holotypes. Those without this indication are all holotypes.

Membracis humilis aurora*
Enchenopa ansera
Tropidoscyta brunneidorsata*
T. binotata
T. maculata
T. immaculata
T. albipes*
T. minuta
Erechtia trinotata
Leioscyta brunnea
L. trimaculata
Enchenopa bifenestrata
Leioscyta pulchella
L. ferruginea
Spongophorus foliatus
Hypsoprora albopicta*
Bolbonota lutea
B. nigrata
B. atitla
Umbonia antigua*
U. immaculata
U. lutea*
Hoplophora rubripes
Ochropepla carinata
Aconophoroides projecta
A. rectispina
Potnia maculata
P. brunneifrontis
Alchisme projecta
A. laticornis
A. pinguicornis
A. spinosa

Nassuna nigrofascia
Orekthophora cornuta*
Cymbomorpha nitidipinnis
Spinodamoides typus
Rhexia maculata
Paragargara nigra*
Aconophora erecta
A coffea
A. brunnea
A. lutea
A. brevicornis
Sundarion nigromacula
Stegaspis viridis
Thuris fenestratus*
Lycoderes triangulata
L. luteus
Mina spinosa
Orekthen osborni
Tylocentrus quadricornis
Campylocentrus nigris*
Centronodus denticulus
C. flavus
Dontonodus serraticornis
Stylocentrus rubrinigris
Flexocentrus brunneus
Horiola fenestrata
Tragopa decorata
T. pubescens
T. brunneimaculata
T. maculidorsa
T. albifascia*
T. biangulata
T. longa
T. luteimaculata
Chelyoidea brunnea
C. fasciata
C. maculata
Tragopa testudina*
Xiphistes maculipennis
Xiphistoides carinata
Emphusis bakeri*
E. rugosus
Centrotypus laticornis
C. parvus
Leptocentrus pubescens*
L. arcuatus
L. manilaensis
L. albolineatus
Leptobelus decurvatus*
Maurya angulatus
Periaman brevifrons
Anchon gunni
A. brunneus
Magura nigra
Platybelus luteus
Evanchon serpentina
E. minuta
E. sinuatus
E. maculatus
Maurya brevicornis
Pantaleon brunneus
Antialcidas erectus
Elaphiceps javanensis*
Nilautama minutispina
Otinotus arcuatus
O. pilosus
Sarritor (Hemicentrus) attenuatus
S. (H.) cornutus
Otinoides pubescens
Hypsauchenia recurva
Pyrgauchenia brevinota
Funkhouserella pinguiturris
F. bulbiturris
Pyrgonota arborea
P. binodis
P. brevifurca
P. sinuata
Centrochares foliatus
Ebhul carinatus
E. notatus*
E. elegans
Cryptaspidia trifoliata
C. nigris
C. longa
C. lustra
C. auriculata
C. minuta
C. pilosa
C. elevata
Centroscelus typus*
C. luteus
C. borneensis
C. concavus*
C. brevispinis
C. brunneus
Xanthosticta pseudocornis
Sipylus nodipennis
S. acuticornis
S. rotundatus*
S. auriculatus
Tricentrus laticornis
T. plicatus
T. aequicornis
T. robustus
T. panayensis
T. manilaensis
T. attenuatus
T. purpureus
T. nigris*
T. decurvatus
T. brevis
T. brunneus
T. spinicornis
T. spininervis
T. acuticornis
T. porrectus
T. forticornis
T. bakeri*
T. attenuicornis
T. albescens
T. fulgidus
T. papuaensis
T. ferruginosus
T. altidorsus
T. nigrofrontis
T. suluensis

T. brunneicornis
T. pubescens
T. banguensis
T. spinis*
T. truncaticornis
T. carinatus*
T. amplicornis
T. obesus
T. taurus
Gargara attenuata
G. minuta
G. sinuata
G. sumbawae
G. projecta
G. penangi
G. triangulata
G. nervosa
G. pinguis
G. rugonervosa
G. irrorata
G. brunnea
G. nigrocarinata
G. maculipennis
G. tuberculata
G. granulata*
G. luteipennis
G. grisea*
G. ornata
G. brunneidorsata
G. rufula
G. dorsata*
G. selangori
G. tigris
G. hainanensis*
G. nodulata
G. brunneifasciata
G. alini*
G. albopleura*
G. hoffmanni
G. lata
G. gressitti
G. flavocarinata*
G. albolinea*
G. tonkini
G. nigra
G. virescens*
G. nodinervis
G. fasceifrontis
G. fragila
G. gracila
G. nigroapica
G. nitidipennis
G. sordida
Ceresa curvicornis
C. occidentalis
C. luteimaculata
C. grisescens*
C. rubra
C. viridilineata*
Stictocephala elevata
Melusina nigriventris
Stictolobus trilineatus*
S. lateralis
S. nitidus
S. marginatus
S. viridis
Micrutalis nigromarginata
Euritia albifasciata
Thrasymedes virescens
Aphetea punctata*
A. nigropicta*
Poppea nitida
P. zebrina
Centrogonia pinguicornis*
Penichrophorus lutea
Antonae nodosa
A. bulbosa
Antianthe chichiana*
Tynelia cerulea*
T. brunnea
Boethoos hirsuta
B. nitida
Lallemandia nodosa
Telamona alta
Carynota maculata
Xantholobus arizonensis
Atymna pilosa
Ophiderma fascipennis
Amastris elevata*
A. peruviana
A. sabulosa*
A. minuta
A. projecta*
A. maculata
A. brunneipennis
A. pacifica
Ecuadoria fowleri
Gelastogonia pulchella
Maturna lloydi
M. maculata
Vanduzea mayana
V. punctipennis
V. decorata

—W. R. Allen.

BOOK NOTICE

THE INTEGUMENT OF ARTHROPODS, by A. GLENN RICHARDS. xvi+411 pages, 65 text figures. Univ. of Minnesota Press. Price, $6.00.

In writing this critical monograph on a subject, concerning which a wealth of diversified research has been done and a great amount of further study is needed to complete a still fragmentary picture of a complex subject, the author's stated purpose has been "to cover the available literature and to synthesize this . . . into a coherent picture of the arthropod integument as one of the primary organ systems of this phylum of animals." Since the author has himself been making significant contributions for the past 10 years on several phases of the several sections of this book, his qualifications to present such a review authoritatively are unquestionable.

The monograph represents the collating of original data and material from critically selected references, some 1800 in number, through the year 1949. It is divided into three main sections: the physical and chemical properties of the insect cuticle and its components, its structure and development, and cuticle permeability, including the penetration of insecticides. The tables are mainly original, each representing a clearly presented summary of related references from widely scattered sources. The excellent line drawings and microphotographs have been reproduced with clarity and distinctness. An index of references, by authors, each followed by a list of pages where it has been cited in the text, as well as a subject index are included for the convenience of the reader.

That a wealth of technical information on so widely a ramified subject has presented in so clear and yet seemingly casual a fashion is testimony to the author's ability to translate clear and bold thinking into graphic form. In this work, Dr. Richards has added, to the inflexible thoroughness of the taxonomist and morphologist, the critical and dynamic views of the active researcher, who has himself boldly attacked several facets of this complicated problem by the use of the techniques of the physicist and chemist. The book is written in a direct, straightforward fashion, with the use of non-technical terms wherever feasible and the inclusion of frequent definitions to guide the reader, where necessary. Included are considerations of such widely diverse problems as the chemical nature of chitin and its breakdown by enzymes, molting, the anatomy of muscle attachment, and the general problem of permeability as well as of permeability of the insect cuticle including the penetration of insecticides. As such, this book will have a wide appeal to biologists in general, and to physiologists, chemists, insect morphologists and economic entomologists in particular. To the graduate student, the critical collating of all the significant information on the insect integument, as well as the carefully selected bibliography (including the important reviews available in each phase of the subject) should make this book a useful and convenient reference work.—M. ROCKSTEIN.

NOTICE TO MEMBERS AND CONTRIBUTORS

The Annals of the Entomological Society of America, published by the Society quarterly, includes the Proceedings of the Annual Meetings and such papers as may be selected by the Editorial Board.

Papers should ordinarily be submitted directly to the Editor. However, they may be submitted to any member of the Editorial Board, especially where such member is particularly qualified in the subject matter of the paper.

Any illustrated manuscripts submitted must be accompanied by finished illustrations which are ready for reproduction (or by engravings plus proof if the author prefers to have his own made). The price of zinc cuts or half-tone engravings will be charged to the author at cost. It is to be noted that text, tables, zinc cuts and half-tone engravings are all printed alike on one quality of paper at the standard 4¼ x 6¾ inch size. If an author has tabular material or illustrations that require another size or a special paper, such is obtainable only by special arrangement with the editor and at the expense of the author.

Acceptable style and format depends to some extent on the subject matter to be treated. Authors are referred to recent issues of the journal for the usual styles.

Since the Annals is not a copyrighted journal, permission to quote or to use illustrations is within the province of the author or authors.

Authors will be allowed a total of fifty (50) reprints gratis; additional copies may be ordered at cost at the time proof is returned to the editor.

Members failing to receive their numbers should present the complaint to the Managing Editor within four months from the date of the mailing of the issue. After that time the numbers will be furnished only at the regular published rate. Request for information as to membership and annual dues of members should be sent to the Secretary-Treasurer, Dr. Herbert H. Ross, Illinois State Natural History Survey, Urbana, Illinois.

SUBSCRIPTION RATES AND BACK NUMBERS

The regular subscription rate for the ANNALS is $6.00 (U. S. money) in the United States and all other countries.

Subscriptions from non-members, and orders for back numbers, are now being handled through the Columbus office. Letters should be addressed to Mrs. Helen S. Lanman, Dept. of Zoology and Entomology, The Ohio State University, Columbus 10, Ohio.

The stock of back numbers of the ANNALS is now in charge of The Spahr & Glenn Company, 50 East Broad Street, Columbus 15, Ohio, by whom all shipments will be made, but orders should be addressed to Mrs. Helen S. Lanman as above.

Back numbers are furnished at the following prices: Volumes 1 to 31, $4.00 per volume, $1.00 per issue; Volumes 32 to 38, $5.00 per volume, $1.25 per issue; Volumes 39 to 43, $6.00 per volume, $1.50 per issue.

THE THOMAS SAY FOUNDATION

Vol. I—*Sarcophaga and Allies of North America* . . . . . Price, $3.00
By J. M. ALDRICH

Vol. II—*Plecoptera or Stoneflies of North America* 5.00
By J. G. NEEDHAM and P. W. CLAASSEN

Vol. III—*Plecoptera Nymphs of North America* 4.00
By P. W. CLAASSEN

Vol. IV—*The Blowflies of North America* 6.50
By DAVID G. HALL

Members of the Entomological Society of America will receive a ten percent discount on volume IV, if the purchase is a personal one.

Send orders to J. J. DAVIS, Purdue University, Lafayette, Indiana.

Orders outside the United States, Canada, Mexico and U. S. Possessions, 50 cents extra per volume.

All accounts with the Entomological Society of America, or its Journal, "The Annals," owing by individuals or institutions without the United States should be paid by Postal Money Order in American Dollars.

CONTENTS OF THIS NUMBER

PAGE

HYLAND, KERWIN E., JR.—Observations on the Chigger Mite *Trombicula* (*Eutrombicula*) *splendens* Ewing(Acarina Trombiculidae) 297

TALBOT, MARY—Populations and Hibernating Conditions of the Ant *Aphaenogaster* (*Attomyrma*) *Rudis* Emery (Hymenoptera: Formicidae) 302

EXLINE, HARRIET—*Tegenaria agrestis* (Walckenaer), a European Agelenid Spider Introduced into Washington State 308

CHANG, PEH-I—The Action of DDT on the Golgi Bodies in Insects Nervous Tissue 311

ROBACK, SELWYN S.—A Classification of the Muscoid Calyptrate Diptera 327

BRELAND, OSMOND P.—The Immature Stages of *Aedes infirmatus* Dyar and Knab with Notes on Related Species (Diptera: Culicidae) 362

ROEDER, KENNETH D., AND ELIZABETH A. WEIANT—The Effect of Concentration, Temperature, and Washing on the Time of Appearance of DDT-Induced Trains in Sensory Fibers of the Cockroach 372

HOLWAY, R. T., W. A. MITCHELL, AND ABDEL AZIZ SALAH—Studies on the Seasonal Prevalence and Dispersal of the Egyptian Housefly. I. The Adult Flies 381

FAIRCHILD, G. B., AND MARSHALL HERTIG—Notes on the *Phlebotomus* of Panama (Diptera, Psychodidae). VII. The Subgenus *Shannonomyina* Pratt 399

FAIRCHILD, G. B., AND MARSHALL HERTIG—Notes on the *Phlebotomus* of Panama (Diptera, Psychodidae). VIII. Two New Species of *Warileya* 422

WILLIAMS, ROGER W.—The Immature Stages of *Culicoides tristriatulus* Hoffman (Diptera, Heleidae) 430

FAIRCHILD, G. B.—Descriptions and Notes on Neotropical Tabanidae 441

SIEBURTH, JANICE F., MARY GAIL BONSALL, AND BARBARA A. MCLAREN—A Simplified Biological Assay Method Using the Cockroach, *Periplaneta americana* (Linn.), for Protein Utilization 463

ROCKSTEIN, MORRIS, AND LEONARD LEVINE—Enzymes in Insects. Acid Phosphatase 469

GAUL, ALBRO T.—A Glossary of Terms and Phrases Used in the Study of Social Insects 473

The Funkhouser Collection of Membracidae 485

Book Notices 301, 310, 326, 361, 380, 398, 462, 488

PRINTED IN THE UNITED STATES OF AMERICA
THE SPAHR & GLENN COMPANY, COLUMBUS, OHIO